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SOME AMERICAN ARBORESCENT LYCOPOD FRUCTIFICATIONS¹

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INTRODUCTION

Among the more abundant elements of Carboniferous fossil floras are the fructifications of the arborescent lycopods. Although usually detached, specimens in organic connection with vegetative stems have been found, and there is considerable information available for the various organ genera to which they have been assigned. The strobili present a varied assemblage consisting of bisporangiate specimens and unisporangiate ones containing either microspores or megaspores.

A problem confronting the worker is the identification of microsporangiate fructifications. The megasporangiate ones do not pose a comparable problem, for diagnostic generic characters are usually well-defined, and recent spore studies have contributed materially to a better comprehension of generic boundaries.

Lepidostrobus, *Lepidocarpon*, *Mazocarpon*, and *Sigillariostrobus* have generally been accepted as being well defined, with the first three well represented in North American petrifications, but it is probable that many microsporangiate representatives of these now bear erroneous names. Inasmuch as the fructifications are seldom found attached to vegetative correlatives, identification depends upon characters of the cones. For example, there is evidence that all cones of *Lepidostrobus* may be bisexual, but a number of microsporangiate strobili have been assigned to the genus. Thus, the worker must distinguish these from microsporangiate cones which are definitely known to represent the other three genera listed above. This has proven, in a number of instances, to be rather difficult, and generic limits are not as strongly defined as previously considered. Structurally, these four genera are rather similar in consisting of a central axis bearing whorled or spirally arranged sporophylls, each with a single sporangium on the upper surface. The size range is variable and not a reliable criterion for identification.

¹An investigation carried out in the Henry Shaw School of Botany of Washington University and submitted as a thesis in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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The present study is undertaken with the object of clarifying generic limits of American representatives and of presenting new material which will increase our knowledge of the various cone genera.

The genus *Lepidostrobus*, a uniform one in most respects, is the most abundant American lycopod strobilus. Several species found in the petrified state both in Europe and North America are fairly well known, but in North America the majority of specimens reported have been preserved as impressions and compressions, only a small number of petrifications having been described. The fragmentary and poorly preserved condition of the specimens has rendered it difficult to define specific limits with the clarity desired. *Lepidostrobus* has become a rather general repository for cones believed to have been borne on *Lepidodendron*. It is a heterogeneous assemblage in which specific limitations are difficult to determine and in all probability may include more than one genus. Consequently, the student of the lepidostrobi is confronted by Williamson's ('93) statement: "I have for many years endeavoured to discover some specific character by which different *Lepidostrobi* could be distinguished and identified, but thus far my efforts have been unsuccessful."

This study of American lepidostrobi is not intended to be monographic in scope. Rather it represents an analysis of several American fossils whose mode of preservation has revealed anatomical and spore characteristics of possible value in defining generic limits. The number of American species preserved as petrifications and casts is small in comparison to the number known from Europe, yet the American group includes a varied and distinct assemblage.

Lepidostrobus is an elliptical or cylindrical cone varying from less than 1 cm. to more than 7 cm. in diameter, and from 3 cm. to possibly 50 cm. in length. Structurally, it consists of a central axis with sporophylls arranged spirally or whorled. The stele may or may not be medullated and has a typically lepidodendroid xylem cylinder. Each sporophyll bears a single sac-like sporangium attached its full length to the upper surface by a narrow base. The microsporangia are borne on the upper sporophylls and megasporangia on the lower.

A sizeable collection of cone material has been accumulated in this laboratory in recent years. Specimens of *Lepidostrobus* constituting a new species occurred in great abundance and were in such excellent preservation as to afford valuable information on spore and other anatomical features of the genus. Several specimens are closely comparable to *Lepidocarpon* microsporangiate cones and add to our limited knowledge of these fructifications. In addition various data on other American strobili are compiled.

The specimens came from Mineral, Kansas, and New Delta and Nashville, Illinois, but the most prolific source was the Petersburg V coal north of Booneville, Indiana.

Lepidostrobus has received extensive treatment. Early descriptions were given by Hooker (1848) and by Binney (1871). Notable anatomical studies were made by Maslen ('99) and A. Arber ('14), while the upper Carboniferous British

impression species were reclassified by E. A. N. Arber ('22), who used the shape of the sporophyll as a specific unit of classification.

Lepidostrobus Brownii (Unger) Schpr. is one of the most studied members of the genus. Bower ('93) made a detailed study of the axis, while Zeiller ('09, '14) contributed noteworthy anatomical studies of the species. In North America several species based on compression and impression materials have been described, but only in recent years has attention been turned to lepidostrobi preserved by other means. *Lepidostrobus coulteri* Coulter & Land is regarded as the first petrified example (Tilton, '12). Several other species, including two new ones presented in this paper, have since been described and have contributed materially to our knowledge of the genus.

DESCRIPTION OF NEW SPECIES

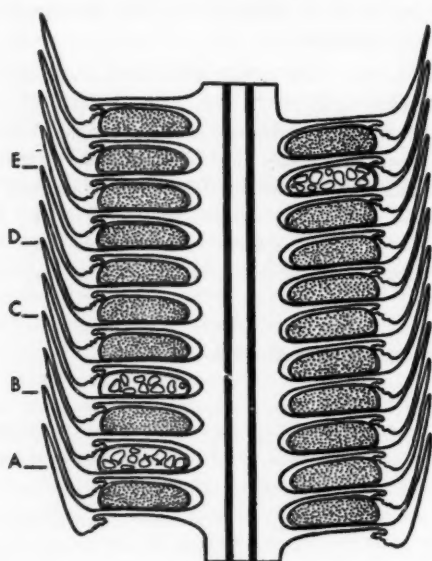
LEPIDOSTROBUS diversus Felix, sp. nov.

This species is based on several specimens in coal balls from the Petersburg V coal near Booneville, Indiana. Numerous strobili, or fragments of them, were found in several coal balls, one yielding several scores of cone axes.

Three specimens are cited as the type and are supplemented by information obtained from eleven others. They were mostly incomplete, but several basal and apical portions were available, and one cone (pl. 14, fig. 7) probably represented an entire strobilus. Five specimens contained megaspores only, four were bisexual, and the remainder contained only microspores. Over a score of fragmented and sporeless specimens furnished data on axial and sporophyll anatomy. None of the specimens were found attached to vegetative shoots, but the longest cone measured 11.2 cm. in length. The maximum diameter never exceeded 1 cm., indicating a long, slender cone. In more complete cones tapering did not start until approximately 6 mm. from the apex, and then it was abrupt to an acuminate tip covered by the laminae.

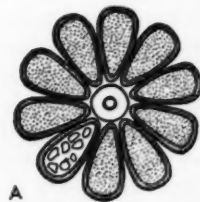
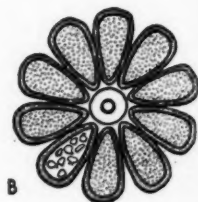
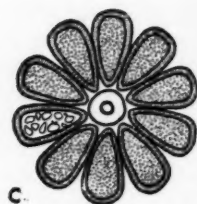
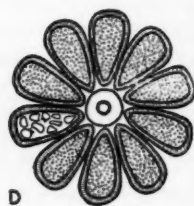
The cones of this species are bisexual with the usual arrangement of megasporangia on the lower sporophylls and microsporangia on the upper ones. An interesting feature is the occurrence of a transition zone, containing both mega- and microsporangia, between the basal megaspore (fig. 12) and apical microspore regions.

The Transition Zone.—A feature somewhat similar to the transition zone has been reported in *Lepidostrobus russelianus* Binney (Chaloner, '53b), and it probably occurs in other lepidostrobi, poor preservation usually limiting observation. *L. diversus* differs from *L. russelianus* in having a zone of intermixed sporangia, best shown in specimens 825 and 857. In the latter clearly delimited alternating zones of megaspores and microspores occurred between the lower megaspore and upper microspore zones. The full length of the zone was not definitely determined due to the fragmentary nature of material, and in more intact specimens the basal sporangia had dehisced.



Text-fig. 1

Text-fig. 1. Diagrammatic drawing of long section from transition zone of *Lepidostrobus diversus*. WCB 857. A-E indicates sections where megasporangia occurred.



Text-fig. 2

Text-fig. 2. Transverse sections from transition zone of *L. diversus*. WCB 857. A-E relate to comparable sections in text-fig. 1.

In specimen 857 six megasporangia were encountered in a space of nine spirals. The megasporangia did not appear in any regular sequence other than occurring in alternate spirals. Only one megasporangium was present in each, with the exception of the sixth which contained two (pl. 13, fig. 5; text-fig. 2E).

The first megasporangium is shown in fig. 1 (pl. 13) and represents section A in text-figs. 1 and 2. Portions of eleven megaspores are visible in the next highest megasporangium in fig. 2, which corresponds to section B of text-figs. 1 and 2. A third sporangium is revealed by section C, and three megasporangia become visible in longi-section (fig. 3), with the basalmost one being the single one shown in fig. 2 and text-fig. 2B. A fourth megasporangium of the spirals is produced by section D and is the uppermost one in pl. 13, figs. 3 and 4; the basal sporangium of figs. 2 and 3 has passed out of the plane of section, and the megasporangia figured in fig. 4 are the two upper ones of fig. 3; and, although in alternate spirals, the obliqueness of the section tends to make them appear to be in adjacent ones. The only spiral of the transition zone containing two megasporangia is the sixth one shown by section E of text-fig. 2 and in fig. 5 of pl. 13; the fifth megasporangium is the uppermost on the left side of the axis, the sixth appearing on the right side of the axis (fig. 5); the lowermost megasporangium of fig. 5 is the upper one shown in fig. 4.

The Axis.—Most of the cone axes measured about 2 mm. in diameter, and possessed a stele composed of primary wood and a small pith. Cortical tissue was seldom preserved. The more complete specimens showed variation in axis diameters from 1.2×1.5 mm. to 1.8×2.9 mm. The stele itself varies from a protostele of 250μ in diameter to a siphonostele of as much as 500μ , the latter containing a pith 60 to 200μ in diameter.

TABLE I

MEASUREMENTS OF VARIOUS ANATOMICAL COMPONENTS OF SEVERAL SPECIMENS

Specimen	Spores in transverse section	Axis diameters (mm.)	Xylem diameters (μ)	Pith diameters (μ)	Xylem width (μ)	Cone diameters (mm.)
810 B/T3	Microspores	1.9×2.5	283×336	110×114	88	4×9
811 A/T2	Microspores	2.1×2.6	336×356	116×132	110	6×9
816 AA/T1	Microspores	1.8×1.9	367×375	66×101	107	6×11
816 AA/B1	Microspores	1.9×2.2	367×448	None	—	4×9
857 B-4	Mega- and microspores	1.3×1.8	331×362	178×224	110	6.9
806 B/T4	Microspores	1.8×1.2	240	63	84	5×7
846-1	Megaspores	1.2×2.4	398×510	219×275	127	5.5×12

The basal regions of the cones contained no pith, and it appears that medullation did not occur until almost half the length of the axis. The pith cavity gradually increased in size, reaching its maximum diameter near the apex. Table I shows the wide variation with regard to size and anatomy of the axes.

In medullated steles the xylem was ringed by a row of exarch protoxylem elements $6-18\ \mu$ in diameter. Within these there are usually four rows of metaxylem cells $22-45\ \mu$ in diameter, with the largest cells restricted to the two innermost rows.

It has been pointed out frequently that size and stelar anatomy are features of the lycopods which must be treated with caution (Arnold, '40; Felix, '52). Several species of *Lepidodendron* and *Lepidostrobus* have been described in which the feature of a protostele or siphonostele has been considered as diagnostic (Hirmer, '27; Mathews, '40). However, it is becoming more apparent, as our knowledge of this group increases, that the xylem-pith relationship is often determined by ontogeny.

Specimen 816 (pl. 14, fig. 7), the most complete encountered, gave some explanation for variations observed (Table II). Here there was some increase in stele diameter from the base to the apex, and most of the cone was protostelic, developing a pith only in the upper microsporangiate region. Campos ('25) found a similar situation in *Lepidostrobus Masleni* in which the axis diameter decreased from base to apex, while the pith diameter increased. The entire cone was medullated, but the possibility that its basalmost portion was missing would account for the failure of a transition to a protostele.

TABLE II
ANATOMICAL MEASUREMENTS OF A SPECIMEN AT DIFFERENT LEVELS

	816 A1 73 mm. from apex	816 A3 46 mm. from apex	816 A4 6 mm. from apex
Axis diameters (mm.)	1.8 x 2.9	1.7 x 2.5	1.8 x 2.1
Xylem diameters (μ)	357 x 428.4	311 x 357	331.5 x 357
Pith diameters (μ)	None	None	76.5 x 112.2

The Sporangia.—The sporangia show no significant departure from that characteristic of *Lepidostrobus*. They are radially elongate and attached adaxially on the narrow pedicel. In tangential sections they are bag-shaped, broader than the pedicel, and overlapping it. They are 3–3.5 mm. long, 0.7–0.9 mm. high, and 2–2.5 mm. wide when mature. Near the cone's apex they decrease progressively, and sporangia 0.5×2.0 mm. contain spores in tetrads. The palisade wall cells of micro- and megasporangia appear identical, varying from $45\ \mu$ in the upper side to $65\ \mu$ near the pedicel.

A small plate of sterile tissue occurs in mature sporangia (fig. 10). Arising

from the base of the sporangium, it is attached radially along the pedicel and frequently presents a T-shaped process. Such a sterile plate is of common occurrence in lycopod cones.

The Sporophylls.—These are attached to the axis in close spirals, usually 10 sporophylls in each. Specimen 816 had 49 spiral revolutions in 83 mm. of cone exposed in sectioning. The adaxial angle of the sporophylls to the axis is about 90° . It was noted that different angles of attachment were found on the same axis, some pedicels being borne at right angles and some pedicels and sporangia arched. This arching has been interpreted as a specific character (Hirmer, '27, p. 191; Hoskins and Cross, '40, p. 424), but here it is evidently caused by varying degrees of distortion. Different angles of sporophyll inclination have been observed in other species, and it was probably a character of the living plant in some instances and not a result of compression. *Lepidostrobus noei* shows such a condition, and Mathews ('40) considered the normal inclination to be near 90° , but in the lower portion of the cone it was 70° and in the upper part 80° .

The length of pedicel from its point of attachment to the axis to the point where it turns upward as a lamina, is about 3.5 mm. Near the apex, pedicels as short as 2 mm. often bear sporangia with mature microspores, and basal ones may attain a length of 4 mm. The pedicel is triangular in cross-section at its point of departure from the axis (fig. 8), being approximately $530\ \mu$ in width, $460\ \mu$ in height, and without an elongated dorsal keel, and as it continues its distal course it becomes flattened laterally. At a distance of about 1.5 mm. from the axis the average width is approximately $900\ \mu$ and the height $350\ \mu$, and the entire pedicel is bordered by dark, thick-walled cells. Here the vascular trace is surrounded by a sheath $200\ \mu$ in diameter, composed of thin-walled undifferentiated cells. These have a tendency to break down, leaving a round cavity. Often a large gap forms beneath the vascular bundle as a result of the disintegration of these cells. There is no evidence of phloem.

The pedicel wings begin to take form midway between axis and lamina, and the width and height both increase (fig. 9). At 3 mm. from the axis the width is about 2.2 mm. and height 0.57 mm., with 0.30 mm. of the height composed of a rounded heel about 0.24 mm. wide at its widest point. At the distal end of the pedicel, near its juncture with the lamina, a maximum width of 4.8 mm. and a height of 0.52 mm. is reached, 0.44 mm. being the length of the heel. Thus the pedicel is broadly flared out at its distal end (fig. 10), and here the dark, thick-walled cells are restricted to the pedicel wings. At this point the pedicel continues upward as a lamina (fig. 6). The lamina is considerably thickened (0.43 mm.) at its juncture with the pedicel and tapers to an acuminate tip. The maximum length is about 6 mm., but near the apex of the cone it may be 2–3.5 mm. long.

At the junction of the lamina and pedicel is a downward projection of the sporophyll, commonly called the "heel". This structure is usually present in *Lepidostrobus* but is absent in the two well-known American species *L. imbricatus* and *L. noei*. The heel in *L. diversus* has an appearance quite different from that of

species previously described. It ranges from 300 to 500 μ in length, is variously lobed, and as many as three or four additional and shorter projections often extend downward from the pedicel behind the principal distal portion (fig. 6).

The course of the sporophyll trace is unusual enough to warrant attention. In the majority of lycopod cones the traces originate from the stele at an acute angle and maintain this path into the sporophyll. An exception is *L. Binneyanus* reported by Arber ('14), where the sporophyll traces follow an obliquely downward direction in the distal portion of their course from stele to sporophyll pedicel. In *L. diversus* the trace makes the usual departure from the stele at an acute angle. This course is maintained upward through the inner cortex for about 600 μ ; a downward bend of about 70 μ occurs before it resumes its upward course through the outer cortex (fig. 11). The trace appears to enter the second spiral above its point of origin, and it always enters the outer cortex at a point opposite the sporophyll below the one which it ultimately enters.

The trace maintains a horizontal course through the pedicel near the adaxial side. It is composed of a mesarch bundle of about 15 scalariform elements and measures 25–35 μ in diameter. At no point during its horizontal course through the pedicel are transfusion cells associated with the vascular trace or seen to run into the sterile plates of tissue of the sporangia. Distal to the sporangial attachment and in the region of the lobed heel, the trace curves downward and then turns up into the lamina. This downward curve is the "dorsal loop", a feature observed in several lycopod fructifications. The tracheids of the trace are scalariform, and in the dorsal loop and the upturned lamina they are accompanied by several scalariform transfusion tracheids.

Despite excellent preservation in several specimens, there was no evidence of a ligule or ligular pit on the sporophyll.

The Megaspores.—Megaspores of *L. diversus* were abundant, several scores of megasporangia being available for study. The spore count of 16 in each sporangium was confirmed by serial peels and by maceration; by maceration technique spores were loosened from the matrix with dilute hydrochloric acid and removed individually from the sporangium with a 00 artist's brush.

The spores are referable to the Lagenicula section of *Triletes* and conform most closely to *Triletes rugosus* (Loose) Schopf. The separation of *T. rugosus* from *T. translucens* is not too well defined. Schopf ('38b) assigned spores to *T. rugosus* on the basis of a slightly smaller size, thicker spore coat, and coarse surface texture. Dijkstra ('46) assigned them both to *T. rugosus*.

The spores of *L. diversus* are longest in the axial dimension, and prominent apical flaps and arcuate ridges are present (figs. 17–19). The spore surface is rugose. However, in reflected light it appears coarser than it actually is (fig. 19) due to differences in lights and shadows encountered in photographing; also the adherence of some dirt particles render it difficult to distinguish essential features. The walls averaged about 10 μ in thickness, ranging from 8.5 to 15 μ . The

diameter in the axial dimension was 645–795 μ in macerated material. In measurements made from peels the diameters were 400–800 μ .

There has been some confusion in the nomenclature of the apical segments of megaspores of the *Lagenicula* section. Schopf ('38b) defined as vestibule: "the structure thus formed consisting of the elongated and upraised apical portions of the three pyramic segments." In *Triletes rugosus* he stated that no vestibule could be detected. Arnold ('50) and Chaloner ('53b) have chosen to use the term "apical prominence" to describe the neck-like projection characterizing the *Lagenicula* section. The elongate spores of *L. diversus* have such an apical prominence formed by expansions of the contact faces (figs. 18, 19); it ranges from 315 to 380 μ high from the apex to the well-developed arcuate ridges. The suture lines are 240–300 μ long and are delimited distally by arcuate ridges.

Aggregates of tiny globules are frequently found adhering to the megaspore wall (fig. 13). Chaloner ('53b) reported similar aggregates of cuticular material on spores of *T. rugosus* from *Lepidostrobus olryi* and *L. russelianus* and on *Triletes borridus* from *Lepidostrobus dubius*. Arnold ('50) described scattered, minute papillae on *Lagenicula rugosa* (*Triletes rugosus* of Dijkstra); their occurrence was so sporadic that he did not consider it a sufficient basis for specific separation. The appendages on spores of *L. diversus* also occur sporadically, being absent on some spores and occurring irregularly in others. They range up to 10 μ in diameter. These were probably more abundant than the number attached to the spores would indicate. Numerous round globular bodies varying in diameter from 2 to 10 μ occur in all the megasporangia. Resembling fungal spores, they number hundreds in some sporangia and appear identical to the globules attached to the spore walls.

An examination of several specimens suggests that the aggregates of globules may serve as an aid in determining heterospory. Specimen 816 is 112 mm. long, 83 mm. of which was exposed in a radial cut (fig. 7); the remaining 29 mm. was not visible due to its oblique direction in the rock matrix. The upper 26 mm. of the cone is composed of microsporangia while numerous microspores are visible in most of the remaining dehiscent sporangia, and to all appearances the cone is microsporangiate. None of these sporangia contained the cuticular globules. At 44 mm. from the cone's apex in about the 35th spiral, empty sporangia first appear containing large numbers of the globular bodies which were associated with megaspores in other cones. They continue to appear at irregular intervals, indicating a transition zone as in specimen 857 (figs. 1–5). At 73 mm. from the apex, sectioning of the cone revealed a sporangium containing megaspores.

Specimen 898 was an incomplete cone section 29 mm. in length with apical and basal regions missing. It was cut in a near-radial plane, and preliminary examination indicated it to be microsporangiate and composed of 22 spirals; the sporangia of the topmost three spirals are filled with microspores. Although dehiscent, the next ten spirals of sporangia contained enough microspores to indicate their microsporangiate nature. None of these contained the globular bodies. The remaining sporangia were empty, and the cone presented the same microsporous

appearance as did the basal portion of specimen 816. However, in the twentieth spiral serial peels revealed a sporangium containing megaspores referable to *Triletes rugosus* and hundreds of the globular bodies as well as about a score of microspores. Some of the spores were still in tetrads probably having filtered in from other sporangia. A microsporangium in the same spiral was almost filled with microspores but there was not a single example of the globular bodies.

In specimens 825 and 857 all megasporangia were found to contain large numbers of the globules in the transition zones but there were none in the microsporangia. Over 100 megasporangia were examined and found to contain the bodies. Of the hundreds of microsporangia examined, very rarely would a scattering of the globules be found in a dehiscent sporangium containing a few microspores. When preservation apparently took place before dehiscence, the bodies were never present within microsporangia.

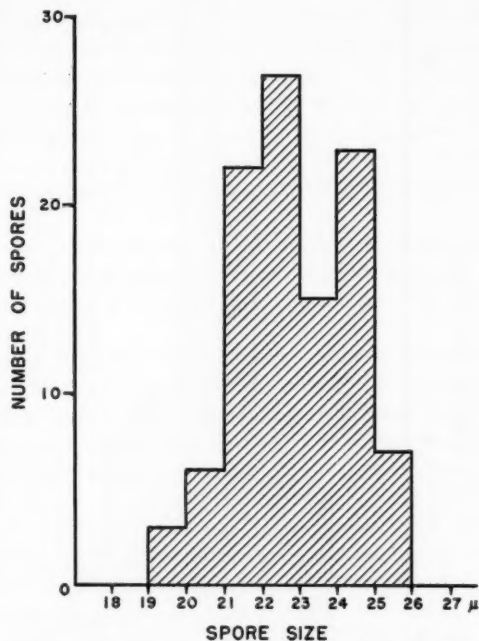
Lepidostrobus noei, an American species in which heterospory has been confirmed, was examined. The megaspores were densely coated with tiny globules 6–10 μ in diameter (fig. 23). The megasporangia contained numerous loose, globular yellow bodies identical to those on the spore wall and similar to those found in megasporangia of *L. diversus*. The microsporangia of *L. noei* did not contain these bodies.

Zeiller ('14) observed minute bodies 3–5 μ in diameter in sporangia of *Lepidostrobus Brownii*. He considered them to be fungal spores but was unable to find any evidence of mycelia. Zeiller reported them as occurring in both megasporangia and microsporangia (p. 40), but his figs. 10 and 20, pl. XI, which show large numbers of them, are of megasporangia.

It is not to be inferred that these cuticular globules can serve as indicators of bisexuality in all cones, but they appear to be reliable where mature mega- and microsporangia are available in the same cone. Their use is limited in that microsporangia occasionally do contain them. They could possibly be tapetal in origin. The immature microsporangia at the cone tip are composed almost entirely of a large subarchesporial pad and contain many large yellow, segmented globular bodies 5–20 μ in diameter; no microspores are present. In successively lower sporangia these segmented bodies break up into small yellow ones similar to the cuticular globules of the megasporangia; simultaneously tetrads of microspores begin to appear. In each successive spiral there is an acropetalous decrease in the yellow globules and a corresponding increase in the number of mature microspores. At the fifth or sixth spiral from the apex the bodies are no longer present and the microsporangia contain only mature microspores.

Bocheński ('39) found similar small granular bodies associated with the microspores in several *Sigillaria* microsporangiate cones. The fact that the spores were in tetrads suggests that the granules might have a tapetal origin.

The Microspores.—The spores, which are referable to *Lycospora*, occurred frequently in tetrads and many microspores are apparently immature. Those described were assumed to be mature, and uniform populations occurred in several specimens (text-figs. 3, 4).

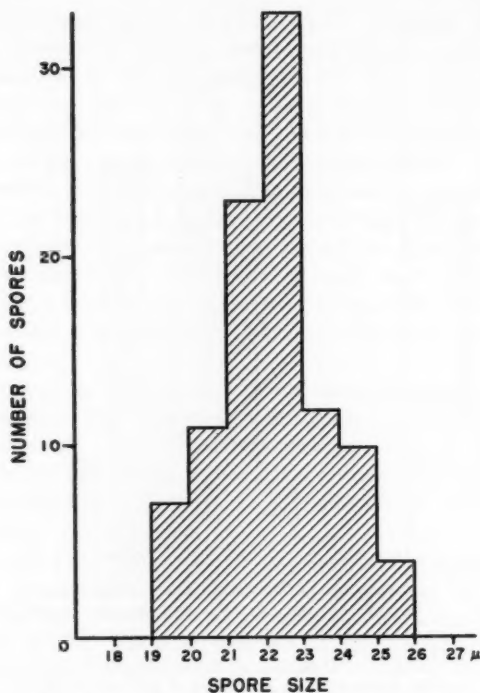


Text-fig. 3. Histogram of microspore size in *Lepidostrobus diversus* from a population of 100 mature spores. WCB 857.

The spores are radial, trilete, and roundly triangular in the transverse plane (figs. 14-16); the holotype measured $22.8\ \mu$ in diameter although other spores range from 19.2 to $25.8\ \mu$. A narrow but distinct equatorial ridge was present, generally $1.2\ \mu$ in width, deviating to $1.5\ \mu$ in only a few instances. The rays are 8 – $11.5\ \mu$ long, and most of them appear to extend to the equatorial ridge. The lips are slightly elevated and about $1\ \mu$ wide with a thin but distinct commissure visible. The spore coat is slightly punctuate on proximal and distal surfaces and $1\ \mu$ thick. No previously isolated spores of *Lycospora* appear to be conspecific with those of *L. diversus*, although *Lycospora rugosa* (Schemel, '51), which occurs in the Des Moines series, has a similar size range but a slightly wider ridge and a granulose to rugose ornamentation.

Associations.—Associated lycopod stem remains were scarce. Five specimens of *Lepidodendron scleroticum* Pannell were found, several specimens of *L. serratum* Felix, and some small (5 mm. diameter) unidentified *Lepidodendron* stems. There is no evidence to indicate that any of these bore the *L. diversus* cones.

Diagnosis.—Cone slender, less than 1 cm. in diameter, approximately 12 cm. long; axis about 2 mm. in diameter, medullated apically but often protostelic



Text-fig. 4. Histogram of microspore size in *Lepidostrobus diversus* from a population of 100 mature spores. WCB 816 A4.

basally; sporophylls arranged spirally, usually 10 per revolution; sporophyll trace bending downward when entering outer cortex, a departure from normal steep upward course; bisexual with microsporangia at apex and megasporangia at base, a transition zone of intermixed mega- and microsporangia between two zones; megaspores 16 to sporangium, 645–795 μ in diameter, assignable to *Triletes rugosus*; microspores numerous, small, 19–26 μ in diameter, mildly punctate with equatorial ridge 1.2 μ wide, assignable to *Lycospora*; ligule not observed.

Locality and Horizon.—Strip mine near Booneville, Indiana; Petersburg V coal, Des Moines series, middle Pennsylvanian.

Type specimens.—WCB 816, WCB 818, and WCB 857, Washington University, St. Louis, Missouri.

LEPIDOSTROBUS pulvinatus Felix, sp. nov.

This description is based upon a single specimen in a coal ball from Mineral, Kansas. It was in excellent state of preservation and only slightly altered by compression (fig. 24). It measured 2×3.7 cm. in diameter and 5 cm. in length. This represents only a portion of a large lycopod fructification.

The sporangia, all containing microspores, possess a massive parenchymatous tissue developed to a greater degree than has been observed in any lycopod strobilus other than the megasporangiate one of *Mazocarpon*. The specimen represents the most significant lycopod fructification found in Mineral coal balls. The paucity of such cones has been made more apparent by the fact that the arborescent lycopods were one of the most abundant elements (Andrews, '51; Felix, '52), and probably no American coal ball deposit has produced larger quantities of *Lepidodendron*.

Stelar Characters.—The central vascular cylinder is enclosed by the tissue of the axis, little cortical tissue being preserved. The stele measures 1.3×2.2 mm. in diameter, the pith being 0.46×1.4 mm. in diameter. There is no evidence of tracheidal cells in the pith.

The xylem width is about 380μ . The metaxylem is five rows in width with the larger cells $65-85 \mu$ in diameter and the protoxylem elements $11-15 \mu$. The large xylem elements possess wall thickenings which depart slightly from a strict scalariform arrangement. The bars are $3.5-4.2 \mu$ thick and branch quite regularly to present a somewhat reticulate appearance such as is often found in lycopods but only to a limited degree. *L. pulvinatus* differs in that most metaxylem elements show this feature. "Williamson's striations" are present in all xylem elements.

The Sporophylls.—The sporophylls form a close spiral about the axis, and the angle of attachment is about 90° . The pedicel is about 16 mm. long from axis to lamina. It increases laterally from about 1.2 mm. near the axis to a maximum width of some 3.5 mm. at a point 2 mm. from the distal end. The upturned lamina measures over 17 mm.

The trace originates from the stele at an acute angle, maintaining this course to the sporophyll. In its course through the pedicel it is mesarch and composed of 20-25 xylem elements which average $60-85 \mu$ in diameter. It is accompanied by numerous transfusion cells, and all trace elements are surrounded by a sheath $45-75 \mu$ wide composed of thin-walled cells. The protoxylem cells are $6-7 \mu$ in diameter; those of the metaxylem $13-20 \mu$.

Parichnos strands run the length of the pedicel, one on either side of the trace. They are formed at the proximal end of the pedicel by a bifurcation of parenchymatous tissue accompanying the trace. The strands are $160-205 \mu$ in diameter, each composed of 10-12 large thin-walled cells $35 \times 45 \mu$ to $44 \times 66 \mu$ in diameter. The parichnos is adjacent to the parenchymatous tissue of the sporangium and often difficult to distinguish due to similarity of their tissues.

Although a ligular pit appeared to be present on some sporophylls, no definite ligulate structure was observed.

The Sporangia.—The sporangia have the radially elongated, narrow attachment to the pedicel characteristic of the lycopods. They are about 14 mm. long and 3.5-4 mm. high. They taper from 1.2 mm. wide adjacent to the axis to 5 mm. near the distal end, and are somewhat wedge-shaped when viewed transversely (fig. 28). Each sporangium is attached to the pedicel by a narrow neck of tissue

about $65\ \mu$ in height and $175\ \mu$ in width. The sporangia are covered with the palisade layer of cells characteristic of *Lepidostrobis*. The prismatic cell layer varies in thickness; it is thicker at the base ($75\text{--}90\ \mu$), but near the top the sporangium wall is noticeably thinner ($30\text{--}35\ \mu$).

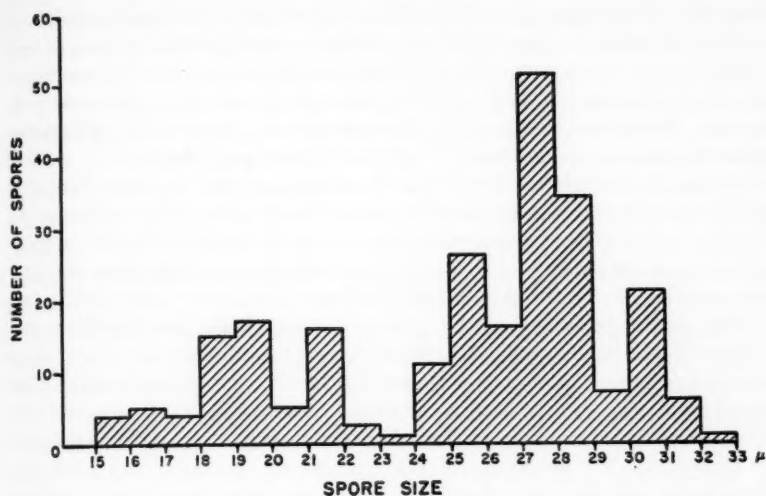
The amount of parenchymatous tissue in the sporangia is a prominent feature; it may appear as a T-shaped plate or swollen pad nearly filling the sporangium (figs. 25–28), or it may be entirely absent. It is not as regular a feature as in the megasporangiate *Mazocarpon* but nevertheless of frequent occurrence in apparently mature sporangia. In those sporangia showing considerable amounts of tissue the pad often extends 3.7 mm. into the sporangium and nearly fills it laterally. The basal cells of the pad are loosely arranged, irregular in shape (fig. 29), and measure $40 \times 217\text{--}102 \times 170\ \mu$. Cells in the upper part of the pad are smaller, more compactly arranged, and more nearly isodiametric (fig. 30), being $54.5 \times 68\text{--}80 \times 85\ \mu$ in diameters. Many lateral plate-like branches occur, and large groups of spores are often almost completely embedded in the central bulk (figs. 25, 26). Several layers of elongate thin-walled cells are preserved internal to the columnar cells of the sporangial wall. These layers apparently line the entire sporangium wall and are $75\text{--}90\ \mu$ wide in various sporangia.

Several of the sporangia show a development of the central plates of tissue which extend across them in a manner similar to the trabeculae of *Isoetes* (figs. 27, 28). In *Isoetes* these are a result of sterile cells which form in the sporogenous tissue. Here the irregular development of lateral plates appears to be due to a breakdown of the parenchymatous tissue. No spores or abortive material are ever present in the cavities.

Bower ('03, p. 197) has pointed out the various conditions in which sporangeous tissue occurs in living spore producers. In many plants disorganization of a portion of the tissue occurs without becoming fertile (forming tetrads) and the subsequent absorption of the cells by the developing spores. Too, the sterile cells often persist as permanent tissue, sometimes forming partial or even complete septa.

There have been numerous arguments, based upon comparisons of habit, leaves, stem, and underground organs, in favor of the derivation of *Isoetes* from the Lepidodendraceae. Bower favored the derivation of *Isoetes* from the Lepidodendraceae due to the resemblance between the trabeculae of *Isoetes* and the sterile plates of tissue of lepidostrophi sporangia. The sterile plates of lepidostrophi originate from the subarchesporial pad as outgrowths and show no connection with the upper sporangial wall, as do the trabeculae of *Isoetes* which result from sterilization of potentially sporogenous tissue.

The Spores.—All of the sporangia contained microspores which were assignable to *Lycospora*, and spores from a single sporangium showed considerable variation (pl. 17, figs. 32–45). Spores in the upper part of a sporangium above the central pad were abortive in appearance. Usually withered, they were mixed with large numbers of globular, resin-like bodies. A considerable number from this region



Text-fig. 5. Histogram of microspore size in *Lepidostrobus pulvinatus* from a population of 250 spores obtained from a single sporangium. WCB 917.

were among the smallest isolated but showed distinct, and presumably mature, ornamentation features, ridges, and sutures (figs. 39-41).

The spore size varied widely (text-fig. 5). The largest spores occurred at the base in the sporangium (figs. 31, 34); their preservation was poorest, and they were compacted into dense masses often nearly completely enveloped by lateral projections of the central tissue. A large population consisted of probably mature spores whose diameter ranged from 25 to 31 μ (figs. 32, 35, 45). About 60 per cent of the spores were in this group. The spore coat was 1.2 μ thick, and the equatorial ridge 3.6-4 μ wide. The spores were coarsely punctate proximally and distally. In many instances a slight translucence was visible along the outer border of the ridge. Sutures were 9-12 μ long, 1.2 μ wide, with narrow commissures and slightly elevated lips.

Approximately 10 per cent of the spores had a size range of from 15 to 19 μ in diameter (figs. 40-42). The larger spores described above are evidently the normal mature form; however, if found isolated, this smaller group would probably be considered mature inasmuch as the spores are not withered or shriveled as they would be if abortive. Ornamentation is distinct, and well-developed equatorial ridges and rays are present. The ornamentation is coarsely punctate proximally and distally as on the largest spores. The equatorial ridge is often lacking on these smaller forms (fig. 42), but when present it is 1.2-1.5 μ wide, occasionally 2 μ , and slightly translucent on the outer margin. The cell wall is about 1 μ thick. The rays are 6.0-7.2 μ long and 1.2 μ wide, with narrow commissures and slightly raised lips. A considerable number of spores in a range of 25-29 μ had no visible

ridge (fig. 33). However, they usually had a withered or shriveled appearance as if atrophied, perhaps accounting for the absence of an equatorial appendage.

Probably 15 to 20 per cent of the sporangial contents are clearly aborted spores and brown globular bodies similar to those seen in immature sporangia of *L. diversus*. Several tetrads occurred in the upper part of the sporangia. These often appeared to be large spores (fig. 43) until seen breaking up (fig. 44).

If found isolated, it is probable that the microspores of *L. pulvinatus* might be assigned to more than one species of *Lycospora*. Among the species diagnosed, the size range of *Lycospora parva* Kosanke (25.1–32.5 μ) is nearest that of the larger population of *Lepidostrobus pulvinatus*. However, their ornamentation and ridge features differ greatly, and there is little likelihood that they are conspecific.

The smaller population of *L. pulvinatus* most closely resembles *Lycospora micropapillatus* (Wilson & Coe) S. W. & B. (15–16 μ) in size and also in many emphytic features. Since most diagnosed species of *Lycospora* and those isolated from known cone species are far larger than *L. micropapillatus*, it is possible that the latter represents immature or aborted specimens such as occur in *L. pulvinatus*.

Discussion.—The assignment of this specimen to *Lepidostrobus* is admittedly questionable, but the great abundance of material from the type locality may eventually afford more tangible evidence of its true affinities. The *Lycospora* type spores are probably not restricted to *Lepidostrobus* alone, yet the unusual sporangia of *L. pulvinatus* offer no close comparison with microsporangiate cones of other lycopod genera. There is also the distinct possibility that the basal megasporangiate region is missing; thus tentatively *Lepidostrobus* appears to be the only genus acceptable.

Diagnosis.—Cone large, incomplete, 2×3.7 cm. in diameter; stele 1.3×2.2 mm. in diameter, pith 0.46×1.4 mm. in diameter and composed of thin-walled cells; sporophylls spirally arranged, prominent parichnos strands running the length of the pedicel; sporangia usually nearly filled with a massive parenchymatous pad which often breaks down to form trabeculae; only microspores present, assignable to *Lycospora* and ranging from 15–33 μ in diameter; no ligule observed.

Locality and Horizon.—Strip mine of the Pittsburg and Midway Coal Company, Cherokee County, Kansas; Fleming coal, Cherokee group, Des Moines series, middle Pennsylvanian.

Type Specimen.—WCB 917, Washington University, St. Louis, Missouri.

RESUMÉ OF PREVIOUSLY DESCRIBED AMERICAN SPECIES

LEPIDOSTROBUS ARRECTUS Hoskins & Cross, in Amer. Midl. Nat. 29:542. 1943.

Lepidostrobus aristatus Hoskins & Cross, in Amer. Midl. Nat. 24:421–436, figs. 3–4, 12, 16. 1940.

Cone.—Medium-sized, 11.5×2.7 cm. Incomplete, both ends missing. Preserved as cast in fine sandstone.

Axis.—Five mm. in diameter throughout known length. Eleven sporophyll bases on axis when viewed in cross-section. Cellular detail not preserved.

Sporophylls.—Arranged spirally, about 11 per revolution and 43 revolutions observed. Adaxial angle of pedicel to axis slightly greater than right angle. Pedicel 1.1 cm. long. Prominent stalk-like sporophyll bases about 1 mm. long on axis. Laminae very wide at base (3–4 mm.), 30–40 mm. long, a portion subtended prominently below the horizontal plane of the pedicel and slightly thickened, tapering rather gradually from wide base to an attenuated tip, closely appressed for the lower half but slightly divergent above, aristate in appearance.

Ligule.—Presence questionable. Indefinite structure arises from distal end of pedicel.

Sporangia.—Borne adaxially on sporophylls, closely crowded, 1 cm. long, wedge-shaped in top view, narrow, but not triangular in cross-section next to axis, broader and somewhat rectangular-ovate at distal end. Narrower pedicel broadly overlapped by sporangia. Apparently attached to sporophyll throughout length by narrow band of tissue.

Spores.—Two sizes found by macerating sporangia: 27 μ and 160–190 μ . Hoskins and Cross compared the megaspores with those of *Lepidostrobus Gallowayi* (Arnold, '33), but the only similarity was in size. A re-examination of megaspores of *L. Gallowayi* has shown that in Arnold's original diagnosis they were probably too small. The spores of *L. arrectus* were not examined in the course of this study, the type slides no longer being extant.

Locality and Horizon.—Pocahontas sandstone, lower Pottsville series, Pennsylvanian system. Six miles northwest of Orleans, Orange County, Indiana; Whetstone quarry.

Material.—One specimen, exposed by splitting sandstone block. Holotype, B-624-section 1 of holotype; B-625-section 2 of holotype. Paleobotanical Museum, Botany Department, University of Cincinnati, Cincinnati, Ohio.

Lepidostrobus aristatus, the original name of this species, was found to be preoccupied. Hoskins and Cross ('43b) proposed the name *Lepidostrobus arrectus*. The name refers to the condition of the attenuated laminae, which overlap, but are not closely appressed and arise at angles of 70° to 80° from the pedicels.

LEPIDOSTROBUS BARTLETTI Arnold, in Amer. Jour. Bot. 17:1028–1032, figs. 1–3. 1930.

Cone.—Entire, 2.5 × 11.5 cm., tapering gradually at both ends.

Axis.—Stele 0.5 mm. in diameter, central pith region surrounded by scalariform tracheids. All cortical tissue decayed.

Sporophylls.—Arranged spirally; pedicel about 1 cm. in length, borne at right angles to axis; lamina slightly more than 1 cm. long.

Ligule.—None observed.

Sporangia.—Dehiscent and poorly preserved; approximately 5 mm. long and 2–3 mm. high; sterile plates of tissue extending into sporangial cavity.

Spores.—Scattered, not found in sporangia; microspores about $20\ \mu$ in diameter; megaspores broadly oval, $735\ \mu$ along largest diameter.

Locality and Horizon.—Shale pit one mile west of Grand Ledge, Michigan. Horizon listed as Pottsville.

Material.—Five ground sections and fragment catalogued as no. 12862 in Museum of Paleontology, University of Michigan, Ann Arbor, Michigan.

Only ground sections of the megaspores were available. The ridges on the spore wall indicate flanges or ear-like lobes similar to *Triletes* which Schopf ('38b) assigned to the section *Auriculati*. However, Dijkstra ('46) placed such spores in the *Aphanozonati*.

LEPIDOSTROBUS BRAIDWOODENSIS Arnold, in Amer. Midl. Nat. 20:709-712. 1938.

Cone.—Incomplete, 35 mm. long, 14 mm. wide; compressed in nodule.

Axis.—No structural details preserved.

Sporophylls.—No structural details preserved.

Ligule.—None observed.

Spores.—One large and 3 aborted megaspores in each megasporangium; axial diameter of large spore exceeds 2 mm., of smaller spores less than 0.5 mm. Granular exine with small spinose appendages. No microspores present.

Locality and Horizon.—Strip mine dump between Braidwood and Coal City, Illinois. Carbondale (Allegheny) age.

Material.—Single specimen in Museum of Paleontology, University of Michigan, Ann Arbor, Michigan.

Arnold ('50) identified the large spore as *Lagenicula saccata*, and, although similar to *Cystosporites giganteus*, it differs in its conspicuous apical prominence and the granular spore wall (fibrous in *Cystosporites*).

LEPIDOSTROBUS COULTERI (Coul. & Land) Jongmans, Foss. Cat. 2: pars 16. 1930;

Mathews, in Bot. Gaz. 102:26-35, figs. 1-2. 1940.

Lepidostrobus Coul. & Land, in Bot. Gaz. 51:449-453, pls. 28, 29, figs. 21-23. 1911.

Lepidostrobus Coul. & Land, in Bot. Gaz. 72:106-108. 1921.

Cone.—Large, 5-6 cm. in diameter, up to 22 cm. long; all specimens incomplete.

Axis.—Tapering slightly, 8-9 mm. in diameter; stele 2.26 mm. in diameter with central tissue undifferentiated; xylem 400-500 μ thick; sporophyll trace collateral, attaining diameter of 400-600 μ in middle cortex.

Sporophylls.—Arranged spirally; pedicel 20 mm. long; lamina 20 mm. long, tapering; prominent heel about 3 mm. long. Parichnos strand accompanying sporophyll trace and bifurcating in pedicel.

Ligule.—Small and between distal end of sporangium and lamina base; sporophyll cells below ligular pit longer than other cells and radiating from pit.

Sporangia.—Attachment entire length of pedicel, 17 mm. long, 2.5-3 mm. broad. Small subarchesporial pad present but no radiating sterile tracts within

sporangium. Palisade cells of wall about $75\ \mu$ high, attaining $125\ \mu$ at corners and decreasing to $25\ \mu$ at point of dehiscence.

Spores.—Scarce, scattered in dehiscent sporangia. Only microspores present, $27\ \mu$ in diameter, frequently in tetrads about $50\ \mu$ in diameter.

Locality and Horizon.—Obtained from coal pocket in small drift mine near Indianola, Iowa. Horizon listed as Pottsville.

Material.—Sections G21, M1-M5 and G21, P1-P11. Botany Department, University of Chicago, Chicago, Illinois.

The specimens are preserved in calcium carbonate heavily impregnated with pyrite. Tilton ('12) reported *L. coulteri* to be the first description of a petrified *Lepidostrobus* from America.

LEPIDOSTROBUS GALLOWAYI Arnold, in Papers Mich. Acad. Sci. 17:51-56. 1932; in Amer. Jour. Bot. 22:23-25. 1935.

A lycopodiaceous strobilus . . . Arnold, in Amer. Jour. Bot. 20:114-117, figs. 1-7. 1933.

Cone.—Specimen not petrified, partly preserved and enclosed in sandstone; attached to 3-inch peduncle 13 mm. in diameter. Strobilus 3.5 cm. in diameter by 10 cm. in length; apex bluntly rounded.

Axis.—Transverse sections not available.

Sporophylls.—Numerous, borne in whorls, 12-20 in a whorl, those in adjacent whorls alternating with whorls about $\frac{3}{16}$ of an inch apart; 10-15 mm. long, borne at right angles to axis.

Ligule.—None visible.

Spores.—Arnold ('33) found microspores of two sizes, approximately $35\ \mu$ and $76\ \mu$ in diameter, and either smooth or slightly rough. He described the megaspore as about $150\ \mu$ in diameter, and with slender appendages. Preservation was so poor as to render assignment to any known group impossible, and even the size was approximate as no complete spores were obtained. More recent preparations³ from the type have produced abundant microspores from the apex. These are clearly *Plani-sporites* Knox and quite similar to microspores of the same genus reported in *Sigillariostrobus rhombibracteatus* by Chaloner ('53c). They were $44-61\ \mu$ in diameter. Megaspores obtained from the base of the cone were numerous and differed greatly from the single one figured by Arnold ('33, fig. 2). None of them bore appendages, and although their condition was such as to prevent an accurate measurement, their diameter approximated $400\ \mu$, considerably larger than the original diagnosis.

Locality and Horizon.—In quarry about $1\frac{1}{2}$ miles northeast of Port Allegany, McKean County, Pennsylvania. Pocono Sandstone, lower Mississippian. It was difficult to assign a definite age to this cone because of uncertainty about the age of the horizon. Arnold described it as presumably upper Devonian on the basis of investigations up to that time. However, Wilmarth ('38), Weller et al. ('48), and Cooper ('42) have assigned the Pocono to the lower Mississippian.

³The author is indebted to Dr. W. G. Chaloner for the spore preparations.

Material.—Single specimen in Museum of Paleontology, University of Michigan, Ann Arbor, Michigan.

Lepidostrobus Gallowayi is something of an enigma among lycopod cones. Originally, Arnold ('33) considered the possibility that it was sigillarian, largely on the basis of the whorled sporophylls. Although there is probably a greater tendency toward a verticillate arrangement in sigillarian strobili than in *Lepidostrobus*, the character has been reported often enough in *Lepidostrobus* to render it of little diagnostic value. Its heterosporous condition seemed to be sufficient grounds for Arnold's placing the cone in *Lepidostrobus*.

There is no satisfactory evidence for the existence of bisexual sigillarian cones. Leclercq ('38) did assign a bisporangiate cone to *Sigillariostrobus*, but Chaloner ('53b) found evidence of contamination in her specimen and indications that the microspores were not the original contents of the cone. He subsequently assigned the cone to *Lepidostrobus dubius*. The small megaspores of *L. Gallowayi* do not suggest sigillarian affinity, and the *Aphanozonati* megaspores which appear to characterize the sigillarians approximate 2 mm. in diameter, appreciably larger than even the largest spores obtained from *L. Gallowayi*.

Lepidostrobus Gallowayi possesses a peduncle about 3 inches in length. Arnold ('33) did not figure it, but an examination of the type specimen has left no choice but to consider it structurally a peduncle. The sporophylls and even the delicate lamina are preserved on all parts of the strobilus, but there is no evidence of appendages ever having been borne on the peduncle. Of course, in the absence of additional specimens, the possibility that the pedunculate stalk is a result of preservation, such as partial defoliation of the cone, must be considered.

The presence of this peduncle-like structure on a cone, which seems to be *Lepidostrobus* on the basis of bisexuality, is important because the manner in which the cones are borne on the plant has been considered a major character. Schopf ('41b) considered, and with good evidence, that *Lepidostrobus* was distinguished from sigillarian cones by the terminal attachment of *Lepidostrobus* to ordinary leafy twigs, whereas the latter were borne on specialized peduncles.

The presence of *Plani-sporites* cannot be regarded as conclusive evidence of sigillarian affinities despite the fact that this spore has been obtained from *Sigillariostrobus rhombibracteatus* Kidston (Chaloner, '53c) and occurred in *Mazocarpum oedipternum* Schopf.

From our knowledge of the spores of *Lepidostrobus* a close relationship seems to exist between this genus and the spore-form genus *Lycospora*. The essential feature of the former is a usually well-developed equatorial ridge, and a size range usually between 18 and 45 μ (Kosanke, '50), although Somers ('52) has reported it with a diameter of 50 μ . Microspores obtained from some species of *Lepidostrobus* have the ridge rather poorly developed (Chaloner, '53b), and it seems that there is a gradient from *Lycospora* to *Plani-sporites* in *Lepidostrobus*; the latter spore differs from *Lycospora* in the absence of an equatorial ridge and a greater size range, 25–130 μ in diameter. Thus, on the basis of these characters, the micro-

spores of *L. Gallowayi* must be assigned to *Plani-sporites*, but the fact that there is a range from typical *Lycospora* to *Plani-sporites* does not permit the definite attribution of either spore to a single cone genus.

It would appear that this cone has definite sigillarian affinities and that Arnold was correct in his original diagnosis, but in the face of rather conclusive evidence against bisexuality in sigillarian cones, assignment to this group must be refrained from. If additional specimens prove to be pedunculate or if its vegetative correlative proves not to be *Lepidodendron*, its generic segregation from *Lepidostrobus* would be advisable.

LEPIDOSTROBUS IMBRICATUS Hoskins & Cross, in Amer. Midl. Nat. 24:427, figs. 1-2, 5-II. 1940; *ibid.* 29:541, figs. 1-2. 1943.

Cone.—Medium-sized, 1.8-2.5 cm. in diameter, over 13.5 cm. long, tip slightly tapered and bluntly conical. Preserved as sandstone cast.

Axis.—Approximately 4-5 mm. in diameter at base, tapering abruptly to 2-3 mm.; 13 sporophyll bases prominent in cross-section. No cellular detail observed.

Sporophylls.—Arranged spirally on axis with approximately 100 revolutions in 13.5 cm.; pedicels inserted at right angles to axis and about 8 mm. long to distal end where lamina curves evenly upward; no heel evident; lamina 1.5-2.0 cm. long, slender, not over 1.5 mm. wide at base, tapering gradually to sharp point, closely appressed, overlapping many laminae above, imbricate in appearance; median nerve prominent.

Ligule.—Definite evidence lacking, possibly due to imperfect preservation.

Sporangia.—Borne adaxially on pedicel, 6-8 mm. long and greatly elongated, wedge-shaped in top view and in cross-section near axis but broadly flattened at distal end and overlapping narrower sporophyll; attachment not distinguishable. Densely crowded vertically and laterally and distorted.

Spores.—Small, 26.5 μ in diameter, triradiate openings present in some; no larger spores found in cone.

Locality and Horizon.—Pocahontas sandstone, lower Pottsville series, Pennsylvanian system. Six miles northwest of Orleans, Orange County, Indiana; Chailleaux quarries.

Material.—Three specimens, one a fairly complete cone, are in the Paleobotanical Museum, Botany Department, University of Cincinnati, Cincinnati, Ohio. B-620, holotype; B-621, 622, 623, paratypes; B-1981, hypotype.

LEPIDOSTROBUS KENTUCKIENSIS Scott & Jeffrey, Scott in Roy. Soc. London, Proc. B 88:435-436. 1915; Scott, Stud. Foss. Bot. 2:159, 3d ed. 1920; Read & Campb. in Amer. Midl. Nat. 21:436, 439, 441. 1939; Hoskins & Cross, in The Paleobotanist 1:233. 1952; Cross & Hosk. in Compt. Rend. Trois. Cong. Strat. et Géol. du Carbonifère, Heerlen 1:116, 120. 1952.

Lepidostrobus Fischeri Scott & Jeffrey, in Roy. Soc. London, Phil. Trans. B205:355, pl. 29, figs. 15-21; pl. 39, figs. 20-23. 1914; Hirmer, Handb. d. Paleobot. 1:230. 1927.

Cone.—Large, 4 cm. in diameter by 8.5 cm. long. Incomplete, both ends missing but some tapering towards apex; preserved as weathered petrified fragment, largely of calcium phosphate and ferric carbonate.

Axis.—Approximately 7.5 mm. in diameter; stele about 1.65 mm. in diameter; central pith zone composed of xylem-like cells, but without scalariform markings, surrounded by narrow ring of exarch xylem with corona points corresponding to leaf traces; leaf traces mesarch with sheath of elongate cells, sheaths of adjacent traces confluent around stele; inner cortex 0.25 mm. thick with interwoven structure, but without gaps; outer cortex about 2.25 mm. thick, of narrow prosenchymatous elements, no clear distinction into middle and outer cortex.

Sporophylls.—Pedicels triangular in tangential view, minimum width near axis 1.5 mm., maximum width about 2.8 mm., 2 mm. high, upper surface with groove and median ridge; pedicels inclined downward from cone apex; vascular bundle (rarely preserved) lying in soft tissue above median ridge. Laminae not preserved.

Ligule.—Not observed.

Sporangia.—Borne adaxially on sporophylls, 17 mm. long and about 2 mm. high; palisade wall 120–180 μ thick; evidence of subarchesporial pad.

Spores.—Only microspores present, $48 \times 60 \mu$ in diameter; tetrads about 96 μ in diameter.

Locality and Horizon.—Described by Scott and Jeffrey as from one mile west of Junction City in Boyle County, Kentucky, and from a nodule layer 20–24 inches thick at the base of the Waverly (lower Carboniferous) and immediately above the Genesee Black shale (upper Devonian). This flora has been considered a Devonian one, but recent extensive study of the plants of the upper New Albany shale by Cross and Hoskins ('52) and Hoskins and Cross ('52) indicates it to be of lower Mississippian age.

Material.—Single specimen. Placed in collection of D. H. Scott, East Oakley House, Basingstoke, England. Duplicate set to E. C. Jeffrey, Harvard University, Cambridge, Massachusetts. None of the type material was made available for this study. It was originally named *Lepidostrobus Fischeri* for Mr. Moritz Fischer, the collector, but the name was found to be preoccupied and Scott ('15) proposed *L. kentuckiensis* after the state in which it was found. Scott and Jeffrey considered *L. kentuckiensis* to belong to the same group of Lower Carboniferous cones as *L. Brownii*, differing from the latter primarily in the structure of the cortex. The central stelar tissue was regarded as undifferentiated xylem rather than typical pith and was similar to the central tissue of *L. Brownii*.

The presence of microspores only does not necessarily indicate homosporry, for the basal portion of the cone, where megaspores would be expected, was missing. Only one small radial section, containing a few damaged microsporangia, was available for study, thus limiting conclusions as to heterosporry.

LEPIDOSTROBUS NOEI Mathews, in Bot. Gaz. 102:35-48, figs. 3-7. 1940; Hoskins & Cross, in The Paleobotanist 1:233. 1952.

Cone.—Incomplete, ovoid; both ends missing from fragment 11 cm. long, varying in diameter from 5.5 cm. in lower part to 7 cm. in upper. Petrified in calcium phosphate nodule.

Axis.—Seven mm. in diameter throughout known length; stele 2 mm. in diameter with central tissue of undifferentiated xylem 300-400 μ wide; sporophyll trace collateral, 100 μ in diameter in axis, composed of more than 30 xylem elements.

Sporophylls.—Mathews gave the sporophyll arrangement as spiral with a 2:51 phyllotaxy, but this may be considered whorled as indicated by his fig. 3A (1940). Lowermost sporophyll 7 mm. long, uppermost 22 mm., inclined at 70° in lower cone, 80° in upper; heel absent; laminae 8 mm. broad, 14 mm. long.

Ligule.—Not observed.

Sporangia.—Attached adaxially along entire length of sporophyll, 20 mm. long, with short, unbranched sterile plates extending into sporangium.

Spores.—Megaspores numerous (several hundred per sporangium) in basal sporangia, smooth with triradiate ridges, 320-375 μ in diameter. Microspores in upper sporangia, 50 μ in diameter, frequently in tetrads 76 μ in diameter.

Locality and Horizon.—Vicinity of Paint Lick, near Cartersville, Garrard County, Kentucky. New Albany shale, lower Mississippian.

Material.—Sections and slides G22, M1-M33. Botany Department, University of Chicago, Chicago, Illinois.

Some uncertainty existed as to the correct age of *L. noei*, and Mathews listed it as either Ohio shale (upper Devonian) or New Providence shale (Mississippian). Hoskins and Cross ('52) appear to have definitely established the age as lower Mississippian. The original type, a "weathered-out" specimen, was considered by Mathews to be preserved in calcium carbonate, but Hoskins and Cross found the medium to be calcium phosphate and that the fossil was indistinguishable from phosphatized plant fossils of the New Albany shale. They are of the opinion that it weathered out of the Sanderson or Bedford formations.

Due to increased interest in lycopod spores, the megaspores were examined in greater detail. They were numerous but difficult to macerate intact from the calcium phosphate matrix. The size is somewhat larger than given in Mathew's original description, being 320-375 μ in diameter, occasionally attaining 400 μ , but still rather small for megaspores. The spores are spherical or nearly so (figs. 20-22), characteristically smooth in general appearance. Microscopic examination revealed large numbers of small granular bodies 6-10 μ in diameter on the spore surface (fig. 23); these occurred in moderate amounts on both distal and proximal surfaces, appearing most abundant along the sutures. The spore coat is about 11 μ thick. Trilete rays are short, 120-150 μ long. Suture lines are distinct, often with moderate lips about 8 μ wide. Arcuate ridges are not distinguishable.

The spores are assignable to *Triletes*, a genus with affinities to the free-sporing lycopods. To the author's knowledge, *L. noei* has not been described as a free-sporing species.

GENERAL CONSIDERATION OF MORPHOLOGY AND EVOLUTION

The Ligule in Lepidostrobos.—A ligule was not observed in *L. pulvinatus* or *L. diversus*, and material of *L. diversus* was sufficiently well-preserved and abundant that the failure to locate the structure was somewhat unexpected. Its absence warrants re-examination of the evidence for ligulate members of the lepidostrobi. Although the ligulate character of *Lepidostrobos* is a generally accepted fact, there are relatively few instances of the positive occurrence of a ligule in the genus. Solms-Laubach ('91) apparently was the first to suspect its existence, his assumption being based on a probable ligular pit scar on lepidostrobi compression material. The first authentic report of the ligule was by Maslen ('98) in slides of *Lepidostrobos oldhamius* preserved in the Williamson collection. A ligular chamber was absent, but a ligule of some 0.5 mm. in length was overarched by the distal end of the sporangium. There was no evidence of tracheids or transfusion tissue in the ligule or between it and the vascular bundle of the sporophyll. There is reason to believe, however, that *L. oldhamius* is actually the microsporangiate cone of *Lepidocarpus* and was borne on *Lepidophloios*. Schopf ('41a) suggested a possible correlation of lepidocarp genera with *Lepidophloios* and also cited statements of Hemingway's to this effect.

There are reports of ligules in specimens definitely assignable to *Lepidostrobos*. *L. Veltheimianus* Sternberg (= *L. Scottii* Jongm.) is one of the better known and is represented in many text-books. Arber ('14) observed several examples in her anatomical study of the genus. Six ligules were figured from an apical section of *L. oldhamius* f. *pilosus*. She reported a ligular pit in several instances in *L. Binneyanus*, but a definite ligule was not evident. In *L. gracilis* Arber (= *L. Arberi* Jongm.) she described a ligule which was sunken in a pit.

Ligules have been reported in *Lepidostrobos Brounii*, the bisexual character of which seems sufficient grounds for lepidostroboid affinity. Zeiller ('09) observed a ligule at the cone's apex, along with a rudimentary sporangium. A ligule was also seen on a lower sporophyll bearing a mature sporangium.

Difficulty encountered in locating ligules may be partially explained by Zeiller's ('14) later work on the species. Several ligules were observed near the cone's apex and borne on the ventral surface of sporophylls in the manner of the ligule of *L. oldhamius*. In mature portions tissue of the ventral sporophyll completely decomposed in the ligular region. Zeiller considered the ligule to be ephemeral, atrophying, and decomposing rapidly. Well-preserved apices of *L. diversus* were available to this writer but showed no evidence of ephemeral ligules.

The existence of an eligulate heterosporous member of the Lycopodiales has never been satisfactorily demonstrated. Walton ('31) urged caution in attempting to establish the existence of eligulate heterosporous Lycopodiales, and he attributed the absence of a ligule in several members to leaf abscission in the region between the ligular pit and stem or to overlapping leaves in foliage-bearing specimens. In known ligulate Lycopodiales no evidence of a ligule remains when the sporophyll

falls. Bode ('29) reported a cone genus *Porostrobus* from paper coals of the Moscow Basin as being eligulate and heterosporous. However, the plant to which he referred *Porostrobus* was demonstrated later by Wilson ('31) to be *Bothrodendron* and ligulate. Bode's interpretation of heterospory was also questioned by Walton ('31) who believed that two size ranges of megaspores were represented, as has been reported in *Mazocarpon shorense* Benson.

Of the ten species of American *Lepidostrobus* treated in this paper only one, *L. coulteri*, possessed a ligule, and its authenticity can be questioned because of the probability of its belonging to the Lepidocarpaceae. On the basis of available evidence it appears there is no indication that a ligule is a constant feature of the genus.

Cone Correlations.—Organic connection is the only reliable means of definite correlation of plant remains. Upon the establishment of a correlation detached specimens may be assigned to parent genera, providing dependable and constant characteristics of identification are present in both specimens. Even though relatively few known species of *Lepidostrobus* have been correlated with *Lepidodendron*, these have been numerous enough to demonstrate affinities of the two, and in *Lepidostrobus* there are examples of attached strobili well enough preserved to permit establishment of dependable characteristics. Consequently, some detached strobili can be accepted as valid representatives of the genus in that they possess distinct characters of those that have been found attached to *Lepidodendron* (i.e. *L. dubius*).

Megaspores are being increasingly used to determine lycopod cone species. Chaloner ('53b) found them to be the only diagnostic character of *Lepidostrobus dubius*, *L. allantonensis*, and *L. russelianus*. The appearance of *Triletes rugosus* in *L. diversus* reflects some doubt on the reliability of such identification alone, for this megaspore has been reported as occurring in *Lepidostrobus russelianus* and *L. olryi* (Chaloner, '53b), and Arnold ('49) figured a cone bearing the same spore. Actually there has been little effort previously to establish a correlation between megaspores and the fructifications which bore them and in turn to attribute the cone to a parent tree. It has only been recently that the value of macerations has been recognized in such correlative efforts, and many early spore preparations exist only as ground, non-serial sections.

Table III lists several megaspore species which have been correlated with lepidostrobi. However, actual instances in which known cone species have been associated with their vegetative correlatives are very few. Among the more reliable are *Lepidostrobus dubius* which has been found in organic connection with *Lepidodendron simile*. *Lepidostrobus russelianus* has been associated with *Lepidodendron acutum* Presl (*sensu* Nemejc). *Lepidostrobus olryi* was probably borne on a lepidodendroid parent plant, but there is some evidence that the parent plant might have been a *Bothrodendron*. The well-known *Lepidostrobus Veltheimianus* Sternberg (= *L. Scottii* Jongm.) has long been considered to be the fructification of *Lepidodendron Veltheimianum* (Kidston, '01, p. 61), but apparently this attribu-

tion was based on association only. Calder ('33) has linked *Lepidostrobos Brownii* with *Lepidodendron Brownii* Unger on similarity of anatomical features. However, proof of organic connection is lacking and such comparisons based on evidence of comparative structures is always rather questionable.

TABLE III
A CORRELATION OF MEGASPORE SPECIES WITH *LEPIDOSTROBUS*

Cone species	Spore	Authority
<i>Lepidostrobos allantomensis</i>	<i>Triletes crassiaculeatus</i>	Chaloner ('53b)
<i>Lepidostrobos braidwoodensis</i>	<i>Lagenicula saccata</i>	Arnold ('38)
<i>Lepidostrobos diversus</i>	<i>Triletes rugosus</i>	Felix
<i>Lepidostrobos dubius</i>	<i>Triletes horridus</i>	Chaloner ('53b)
<i>Lepidostrobos Masleni</i>	<i>Triletes diabolicus</i>	R. Scott ('06)
<i>Lepidostrobos olryi</i>	<i>Triletes rugosus</i>	Chaloner ('53b)
<i>Lepidostrobos russelianus</i>	<i>Triletes rugosus</i>	Chaloner ('53b)
<i>Lepidostrobos zea</i>	<i>Triletes auritus</i>	Chaloner ('53a)
* <i>Lepidostrobos</i> sp.	<i>Lagenicula rugosa</i>	Arnold ('49, '50)

* Assigned to *Lepidostrobos russelianus* by Chaloner ('53b).

Lepidostrobos Jacksoni Arber was attributed to *Lepidodendron obovatum* Sternberg by Arber ('16), but the leafy shoot figured was probably too poorly preserved to justify definite assignment. It is noteworthy that in nearly every instance where cones have been reliably associated with *Lepidodendron*, their megaspores belong to the section *Lagenicula* of *Triletes*, and no strobilus bearing *Lagenicula* megaspores has been assigned to any genus except *Lepidodendron*. An exception is *Lepidostrobos zea* (Chaloner, '53a) bearing the megaspore *Triletes auritus*, which is assignable to the section *Auriculata*. However, on the basis of anatomical and microspore differences, *L. zea* might well deserve different generic status, and there is no evidence that it was borne on *Lepidodendron*.

Dioecioism in Lepidostrobos.—Available evidence indicates that cones of *Lepidocarpon*, *Mazocarpon*, and *Sigillariostrobus* were unisexual. Several species of *Lepidostrobos* with bisexual cones are known, and there is a possibility that all valid species of the genus may be bisexual, but such an assumption cannot be made without an explanation for several unisexual strobili attributed to the genus.

One of the best-known species of the genus is *L. oldhamii* Williamson which was treated by Maslen ('99) in a classic work usually regarded as the most complete account of the anatomy of these cones. The species is considered to be homosporous,

possessing only microspores, but its homospory is debatable due to the fragmentary nature of Maslen's material. Several forms of the species were set up in his study, and in only one was there as many as two sections from the same specimen. From the large number of slides examined from various localities, megasporangia should have been evident if present. Many additional specimens have since been studied without the discovery of a bisexual cone. The possibility, mentioned previously, of *L. oldhamius* being a lepidocarp fructification could explain the absence of a bisexual cone.

On the basis of Williamson's ('93) microsporangiate cone, *Lepidostrobus foliaceus* Maslen (= *L. Masleni* Jongm.) had been considered unisexual. However, R. Scott ('06) found a megaspore, tentatively named *Triletes diabolicus*, in Williamson's type cone as well as in the majority of specimens of this species in Scott's collection. The spore's morphology is still undetermined since macerations are evidently unavailable. The same species was considered by Campos ('25) to be a principal piece of evidence for homospory in *Lepidostrobus*. He possessed a splendid specimen from the Halifax Hard Bed of Huddersfield, Yorkshire, England, which he believed represented the entire cone and he was convinced it contained only microspores. The cone was only 5.1 cm. long, and its average diameter was 2.4 cm., indicating a stubby, ovoid strobilus. Twelve transverse ground sections were made, and it is probable, judging from Campos' description, that he never saw the specimen before preparation. A study of the twelve sections shows that the apex (G1-8) is undoubtedly present, and preservation is so excellent as to leave no doubt but all the sporangia contain microspores. However, Campos based his belief that he possessed the entire cone upon evidence provided by the two lowermost sections (G6-18, 19). They were considered basal because of a converging of the general outline toward the base, the total absence of sporophyll lamina sections on the two lowest slides, and the decreased number of sporangia sections. If truly basal, there could have been no megasporangia present.

An examination of the slides indicated that there is not a converging of sporangia but rather a distortion of arrangement as if by pressure. In upper sections there is a uniform arrangement of numerous stalked pedicels about the axis; this is peculiar to the species due to the oblique angle at which the pedicel departs from the cone axis. In sections G6-18, 19 the arrangement has been lost and the pedicels pushed to one side. In upper sections very few sporangia are distorted and there is little evidence of dehiscence, but basal sporangia are considerably disarranged and broken. As for the total absence of sporophyll lamina, *there are several lamina in the two lowest slides*. Most of them are broken and pushed to one side but are easily recognized by the indiscriminately scattered cells with dark contents (or secretory sacs), which were mentioned as characteristic of the species by Maslen ('99). It is very possible that the base of the cone is missing and subsequently the megaspore region also.

In an emended diagnosis of *Lepidostrobus dubius* Binney, Chaloner ('53b) describes cones containing megasporangia throughout or megasporangia in the basal part and microsporangia at the apex. Inasmuch as the spores in both belonged to *Triletes horridus*, two names of *forma* status were used to distinguish two types of cones. *L. dubius* forma *megalophorus* contained only megaspores, which occupied the cone to the apex. *L. dubius* forma *hermaphroditus* contained megaspores at the base and microspores at the apex.

It has been acknowledged that dioecioism probably existed in lepidostrobi, and *L. dubius* forma *megalophorus* doubtless represents an authentic example.⁴ It is also possible that *L. Masleni* of Campos ('25) was microsporangiate, but characteristics of the genus; particularly those species whose vegetative correlatives have been ascertained, indicate that *Lepidostrobus* consists of bisexual cones.

It is notable that this odd distribution of sporangia may be found in *Selaginella*. Sykes and Stiles ('10) found microsporangia to be rare in *Selaginella Vögelii*. In some cones only one mature microsporangium would occur in association with numerous megasporangia, and occasionally only megasporangia were present in a cone. In her extensive treatment of *Selaginella*, Mitchell ('10) listed four types of sporangial distribution: 1, a single large basal megasporangium, the other sporangia being microsporangia; 2, several basal megasporangia, followed by apical microsporangia; 3, cones wholly megasporangiate or microsporangiate; 4, an indiscriminate arrangement of mega- and microsporangia.

Basically, it appears that *Lepidostrobus* was bisexual, but there is no valid reason why dioecioism could not also have occurred. Examples of irregular spore distribution, such as occurs in *Selaginella* (Duerden, '29), have been recorded among fossil lycopods, and the variation in extant lycopod sporangia arrangement suggests the multitude of possibilities in strobili of this genus which was at the peak of evolution during the Carboniferous.

That such digressions from normal sporangial development do occur in fossil species has been shown by Bocheński ('36) in *Lepidostrobus major*; normally there were one large and three abortive megaspores but there were frequent instances of abnormal spore development consisting of one normal and one abortive, one normal and two abortive, and even one large and 15 degenerated spores (Pl. V, figs. 31, 31a).

Sporophyll Arrangement.—The sporophyll arrangement of the lepidostrobi has lost significance as an important character. It was long considered to be spiral, and Bocheński ('36), among others, suggested the verticillate arrangement as a feature of *Sigillariostrobus*. Chaloner ('53b) found specimens of *Lepidostrobus russelianus* with a whorled arrangement and other specimens with a spiral phyllotaxy. Also, some specimens of *L. dubius* were discovered with whorled sporophylls although most specimens were spiral. Inasmuch as the vegetative correlative of both species

⁴In an interview with Chaloner he told me that he was aware of the importance of this specimen and that great care had been taken to establish definitely its megasporangiate character.

is known to be *Lepidodendron*, both forms of phyllotaxis may occur in the same species.

Zeiller ('14) has reported a verticillate arrangement in *L. Brownii*, and the American species, *L. noei* and *L. Gallowayi*, have a similar phyllotaxy. It is probable that *L. Veltheimianus* Sternberg (= *L. Scottii* Jongm.) is another example of both arrangements occurring in a single species. Williamson ('72) described this species as spirally arranged, while Scott ('20) noted specimens with sporophylls in alternate whorls.

Evolution in Lepidostrobus.—Several workers have considered an evolutionary trend in the lepidostrobi which has led to *Lepidocarpon*. Bocheński ('36) considered *Lepidostrobus major* to be a connecting link to *Lepidocarpon Lomaxi* Scott⁵ in a phylogenetic series to the Lepidocarpaceae. Similarly, Hirmer ('37) regarded *Lepidostrobus major* and *L. Bobdanowiczii* as forms transitional between the free-sporing lepidostrobi and *Lepidocarpon*.

Arnold ('38) suggested that the lageniculate *Triletes* represented a distinct evolutionary trend toward a reduction in megaspore number, with a corresponding increase in spore size; the height of the development was attained by *Lepidocarpon* where the single large megaspore was retained and protected by the integument-like outgrowth. He considered forms such as *L. braidwoodensis* as intermediate between many-spored forms and the *Lepidocarpon* type. It seems quite probable that such an evolutionary trend occurred, but it is unlikely that *Lepidocarpon* was the result. The stratigraphic range of *Lepidocarpon*, as given by Schopf ('41a), is comparable to that of *Lepidostrobus*, and it is well represented throughout most beds containing *Lepidostrobus*. It has been confirmed that *Lepidostrobus* was borne on *Lepidodendron*, while most evidence points to *Lepidocarpon* being the fructification of *Lepidophloios*. However, there is some question whether the leaf-cushion character of these genera are distinctions of generic importance.

Schopf ('41a) was of the opinion that the lepidocarps comprised a family group of natural affinities, and that the differences between the lepidocarp fructifications and those of the free-sporing lycopods were valid criteria for family differentiation. Thus, one of Scott's diagnostic characters, "the development of a single functional megaspore in each sporangium," is now found in two different genera. It would appear that this megaspore has not received the attention it deserves, and many workers have been over-eager to assign large sac-like megaspores to *Cystosporites*. Schopf's ('38b, p. 38) diagnosis of the genus included: "spore coat composed of interlocking matted fibrils, widely spaced and porous in the intermediate zone." He did associate it with the Lepidocarpaceae, though noting later ('41a, p. 555) that it might belong to the Lepidocarpaceae only in part.

In every instance where integumented Lepidocarpaceae (*Lepidocarpon*, *Illinocarpon*) megaspores have been isolated they have shown the fibrous spore coat

⁵Bocheński referred to a *Lepidostrobus Lomaxi* in his text (p. 211). However, there is no such species of *Lepidostrobus*, and *Lepidocarpon Lomaxi* was obviously intended.

(Darrah, '49). To this author's knowledge a fibrous-textured spore has never been isolated from unquestioned lepidostrobi. *Lagenicula saccata*, the single functional megaspore of *Lepidostrobos braidwoodensis*, most nearly approaches the lepidocarp character among the lepidostrobi. However, this spore is no larger than some species in which all the megaspores of a tetrad were functional; it possesses a granular extine (rather than fibrous) and the apical prominence characteristic of the section *Lagenicula* of *Triletes*.

It appears that distinction must be made between *Cystosporites* and those *Triletes* with a single functional megaspore per tetrad. There is no evidence that the lepidocarps contained any seed megaspore other than the fibrous-textured spore, *Cystosporites*. The only notable instance of its being reported in *Lepidostrobos* is by Bocheński ('36) in *L. major* and *L. Bobdanowiczii*, and it has been suggested that Bocheński's material may be referable to *Lepidocarpon* (Schopf, '38a, p. 143; '41a, p. 560). This is quite probable since Bocheński ('36, '39) mentioned *Cantheliophorus* (Bassler, '19) as representing the same type of fructification as *L. major* and *L. Bobdanowiczii*, while Schopf ('41a) noted that *Cantheliophorus* was actually *Lepidocarpon*, misinterpreted because of manner of preservation. Rather than a transition of forms from many-spored lepidostrobi to *Lepidocarpon*, structurally similar forms appear to have arisen independently and attained a comparable level of development.

Forms such as *Lepidostrobos braidwoodensis* seem most likely the developmental height of a *Lepidostrobos* line. That there will probably be additional examples of evolvement to a single functional megaspore is indicated by the recent discovery of *Lepidostrobos monospora* by Chaloner ('54). Its only significant difference from *L. braidwoodensis* is in the ornamentation of its large saccate spore. Both must be included in the lepidostrobi due to the absence of any integumentary organ and because of the granular texture of the spore coat.

Sigillarian Fructifications.—The cone genera *Mazocarpon* and *Sigillariostrobus* have been satisfactorily demonstrated to belong to *Sigillaria*. It has been suggested that the two genera are synonymous. Schopf ('41b) has recognized the evidence favoring such an interpretation, but he would keep them in different genera.

It seems likely that all sigillarian cones were unisexual. Schopf ('41b) discussed this problem fully, and his questioning of the authenticity of Leclercq's ('38) bisexual *Sigillariostrobus sphenophylloides* has proven justifiable by Chaloner's ('53b) assignment of the species to *Lepidostrobos dubius*. Bocheński ('39) has made probably the most comprehensive study of *Sigillariostrobus* in his treatment of *S. Czarnockii* Boch., *S. rhombibractiatus* Kidst., and *S. ciliatus* Kidst. He confirmed the pedunculate character of the genus, and all three species possessed unisexual cones, i.e., microsporangiate and megasporangiate.

Megaspores of cones reliably attributed to *Sigillaria* have been placed in the Aphanozonate section of *Triletes*. *T. glabratus* and *T. mamillarius* are the only two megaspores attributable to sigillarian cones; neither of these are known to

occur in *Lepidostrobus*. Chaloner ('53c) also made the interesting observation that these sigillarian megaspores were more or less concave-convex or saucer-shaped and not spherical. This shape apparently stems from the large central mass of parenchymatous tissue of the *Mazocarpon* sporangium, a feature used to distinguish it from *Lepidostrobus*.

Schopf ('41b) found little specific difference between cones of *Lepidostrobus* and microsporangiate cones of *Mazocarpon oedipternum*. He considered the chief specific distinction to be the pedicel, that of *M. oedipternum* having broad lateral laminae and the pedicel of *Lepidostrobus* being quite contracted. Microspores of *M. oedipternum* are about 60 μ in diameter, significantly larger than those of *Lepidostrobus*. The pedunculate character separating the two has been dealt with previously.

The distinctive feature of *Mazocarpon*, its extraordinary development of intrasporangial tissue, is not characteristic of *Lepidocarpon* or *Lepidostrobus*, and it has been considered that this tissue is sufficient to distinguish microsporangiate cones of the three genera. Benson ('08) did figure a massive intrasporangial pad for microsporangia of *Mazocarpon pettycureuse*, and in *M. shoreense* (Benson, '18) the microspores were supposedly produced in pockets of massive intrasporangial tissue. However, in *M. oedipternum* there is no evidence of intrasporangial tissue in mature microsporangia such as occurred in the megasporangia, and the type slides showed no more sterile tissue than occurs in most lepidostrobi. Immature microsporangia at the cone's apex possessed a large subarchesporial pad, but a similar feature may be observed in most lepidostrobi.

The only reliable criteria at present available for distinguishing the microsporangiate cones from *Lepidostrobus* specimens possessing only microsporangiate features are the broad pedicel and characters of the microspores. The spores are assignable to *Planisporites*, but this form genus cannot be considered as conclusive evidence of sigillarian affinity. However, microspores of both *M. oedipternum* and *M. shoreense* are far larger than any lepidostrobi microspores.

THE GENUS LEPIDOCARPON

The genus was established by Scott ('00) to include fossil seeds which Williamson ('77) had referred to Brongniart's genus *Cardiocarpon*. Scott's original diagnosis was based principally on the presence of microsporangia and megasporangia. Each was surrounded by an integument which completely enclosed the megasporangium except for a slit-like micropyle, and a single functional megaspore was contained in each megasporangium. In a revised diagnosis Scott ('01) omitted mention of the microsporangiate structure, which he had believed to be related to *Lepidocarpon* due to the presence of rudimentary integuments. Other inclusive generic descriptions have been made by Hoskins and Cross ('41) and Schopf ('41a).

Although many species of *Lepidocarpon* have been described in England and America, most workers have studiously avoided mention of a microsporangiate cone, preferring to use characters of the seed-like organ described by Scott. That

such a microsporangiate strobilus was certainly present is evidenced by the absence of a heterosporous *Lepidocarpon* strobilus, although many magnificent specimens have been scrutinized for it. Andrews and Pannell ('42) described a microsporangiate strobilus for *Lepidocarpon magnificum*. Two strobili were found in close association to the seed-like organs. The principal evidence was the great abundance of microspores within the seeds, which are indistinguishable from those of the microsporangiate cones. It was noted, too, that not only were the microspores comparable in size and form but frequently occurred in tetrads in seeds as well as in microsporangia. The two cones revealed no evidence of an integument enclosing the sporangia, and are so typically lepidostroboid that if found alone, they would have almost certainly been classified as *Lepidostrobus*.

Scott considered the *Lepidocarpon* integument as a new organ arising from the superior face of the pedicel and not interpretable as an unfolding of lateral wings of the pedicel. Schopf ('38a) confirmed this interpretation in his treatment of *Lepidocarpon*, and in *Illiniocarpon* he reported the integument as further elaborated and entirely distinct from the sporophyll lamina. Hoskins and Cross ('41) have been the most recent dissenters of this theory and they considered the integument in *L. ioense* to be due to lateral development of the pedicel. However, disputed though its origin may be, this investing structure remains the best diagnostic criterion for the genus.

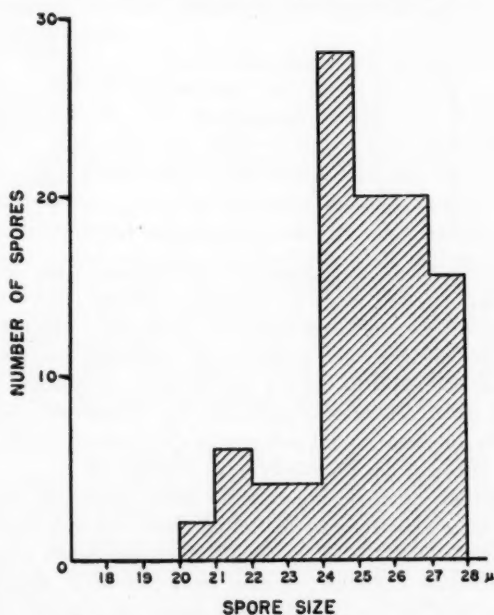
As noted previously, Schopf's ('41a) revised diagnosis featured the relatively enormous megaspore with its fibrous-textured coat. Assignable to *Cystosporites*, there is no question of a partial relationship between it and the Lepidocarpaceae. Since this spore has never been reliably assigned to *Lepidostrobus*, it assumes added significance when evidence of an integument is lacking, a frequent occurrence, particularly in compression material.

Andrews and Pannell ('42) give the microspores of *Lepidocarpon magnificum* as $26\ \mu$ in diameter, and the histogram (text-fig. 6) shows a range between 20 and $28\ \mu$. Spores used were not in tetrads and were assumed to be mature on the basis of ornamentation, ray, and flange characters. The large numbers occurring in tetrads are characteristic of the species, and some difficulty was encountered in isolating sufficient mature spores for the diagnosis and histogram. All are attributable to *Lycospora* and are radial, trilete, and somewhat triangular in a transverse plane (figs. 46-48). The equatorial ridge is quite distinct. In width it averages $2.5\ \mu$ and occasionally reaches $3.5\ \mu$, and the outer portion is clearly transparent. The rays are $9.6-11\ \mu$ long and extend to the equatorial ridge. The spore coat is punctate, the punctations being more pronounced than those of microspores of *Lepidostrobus diversus*. The spores are similar to *Lycospora punctata* (Kosanke, '50) and differ primarily in their much smaller size.

That species assigned to *Lepidostrobus* might be microsporangiate *Lepidocarpon* strobili was suggested by Andrews and Pannell in recognizing the close agreement between *Lepidostrobus coulteri* and *Lepidocarpon magnificum*. Arber ('14) had previously considered *Lepidostrobus oldhamius* as agreeing most closely with *L.*

coulteri. *L. coulteri* and the supposed microsporangiate cone of *Lepidocarpon magnificum* do agree so nearly in all dimensions as to render separation virtually impossible. The microspores are comparable in size, but few specimens of *L. coulteri* contained appreciable numbers of spores, and no macerations of these are available. Comparisons of spores from peels are not reliable and do not show critical features sufficiently well.

There are several specimens in the Washington University collection which are indistinguishable from *Lepidocarpon magnificum* and *Lepidostrobus coulteri*, although they are generally somewhat smaller. Specimens 846, 847, 848, 911, 912, and 918 are from the Booneville (Indiana) locality, and 924 is from Mineral, Kansas. Specimens 23 and 95, of the University of Illinois collection, are in coal balls from Nashville and New Delta, Illinois, respectively. In addition, the Booneville coal balls contained compressed masses of similar large axes and sporophylls intermingled with material of *Lepidostrobus diversus*. These cones attained a considerable length although none of them were complete. Specimen 911 was 9.2 cm. long, 912 over 20 cm., and 924 was 12.3 cm. long. These dimensions compare favorably with the 16 cm. recorded for *Lepidocarpon magnificum* and 22 cm. for *Lepidostrobus coulteri*. Table IV gives measurements of several of these specimens in which good transverse sections were available and affords a comparison with



Text-fig. 6. Histogram of microspore size in *Lepidocarpon magnificum* from a population of 100 mature spores. WCB 166.

L. magnificum and *L. coulteri*. Several of the cones contained microspores, all of them *Lycospora* and resembling rather closely the spores of *Lepidocarpon magnificum* in size range and other morphological features. Spores from specimen 847 are characteristic of those occurring in these cones (figs. 50-53), and tetrads occurred frequently as in *Lepidocarpon magnificum* (fig. 49).

TABLE IV
MEASUREMENTS OF ANATOMICAL COMPONENTS OF SEVERAL LYCOPOD CONES

Specimen	Stele diameter (mm.)	Xylem width (μ)	Cone diameter (cm.)	Axis diameter (mm.)	Pith diameter (mm.)	Horizon locality
<i>Lepidostrobos coulteri</i>	2.26	521.5	5-6	8-9	1.22	Pottsville Indianola, Iowa
<i>Lepidocarpon magnificum</i>	1.4	400	5.0	7.0	0.6	Illinois coal #6 Carbondale, Pennsylvanian Pinckneyville, Illinois
WCB 911	1.1 x 1.5	175	1.3 x 2.6	6 x 6.5	0.7 x 1.1	Petersburg coal #5 Des Moines, Pennsylvanian Booneville, Indiana
WCB 918	1.7 x 2.6	298	2.3 x 5.9	6 x 13	1.1 x 2	Petersburg coal #5 Des Moines, Pennsylvanian Booneville, Indiana
WCB 924	1.1 x 1.3	250	2.1 x 4	3.8 x 6.4	0.67 x 0.78	Fleming coal Des Moines, Pennsylvanian Mineral, Kansas
95a	1.6 x 1.7	230	2.6 x 3.2	6.2 x 6.6	0.92 x 1.8	Illinois coal #6 Carbondale, Pennsylvanian New Delta, Illinois

The reliability of microspores in specific determinations has not as yet been definitely ascertained. These spores are evidently *Lycospora* and within a similar size range but there is no conclusive proof for synonymy. The best positive evidence for synonymy in these cones appears to be the spores, but these are lacking or macerations are not available. Thus, on the basis of available data, it seems most expedient to leave *Lepidostrobos coulteri* in the lepidostrobi subject to further spore studies. The numerous strobili referred to above may be tentatively assigned to *Lepidocarpon*, although not necessarily to *L. magnificum*.

That some of these cones are probably the microsporangiate fructifications is suggested by the close association of several of them with a hitherto undescribed *Lepidocarpon*. Specimen 918 is an apparently microsporangiate cone with empty sporangia, and numerous *Lepidocarpon* seeds are preserved in association with it. Specimen 911 also lies close to many such structures, and it could well be the cone

on which they were borne, for it consists of little more than an axis with several seeds in close proximity.

The *Lepidocarpon* seed organs which occur in considerable numbers and in close association with these cones are characteristic primarily because of the integumentary structure. And though other characters differ little from those of previously described *Lepidocarpon* species, none of the present descriptions are applicable to these specimens.

The seeds occur detached (fig. 55) and are approximately 10 mm. high in the central portion and 10.5 mm. wide at the broadest point. The cells of the sporangium wall are horizontally elongated. One functional megaspore occupies most of the sporangium; its walls are composed of the interwoven fibrils characteristic of *Cystosporites*. The investing integumented structure is distinguished by a dense covering of prominent protuberances which extend from the base to the micropylar slit (figs. 56, 57). The projections are 55–100 μ long and produce a crenate appearance.

LEPIDOCARPON crenatum Felix, sp. nov.

Detached seeds, approximately 10 mm. broad by 10 mm. high; one functional megaspore of the *Cystosporites* type occupying most of the sporangial cavity; investing integumental structure covered by small protuberances 55–100 μ long, giving a crenate appearance.

Locality and Horizon.—Strip mine near Booneville, Indiana; Petersburg V coal, Dr. Moines series, middle Pennsylvanian.

Type specimen.—WCB 816B, Washington University, St. Louis, Missouri.

Two specimens of interest were found in a coal ball of the Mineral (Kansas) locality, deposited in the University of Cincinnati collection (figs. 58, 59). To all appearances they were integumented lepidocarp sporangia containing microspores. The occurrence of such microsporangia would be most unlikely, and the only previous report of such a structure was by Scott ('00) and never actually confirmed. The integument wall of these seed-like organs was 200–215 μ thick and the columnar sporangial wall about 30 μ thick. Several hundred spore-like bodies were enclosed within each (fig. 54). They ranged from 45 to 60 μ in diameter, with walls about 2 μ thick. Peel sections did not show ornamentation or evidence of trilete rays, and numerous maceration attempts failed to isolate anything resembling spores.

That the bodies are not lycopod spores is further suggested by the presence of a prominent megaspore membrane 15–20 μ thick, which upon maceration showed the interlocking fibrils characteristic of *Cystosporites*. The spores are probably fungal, which would explain their poor preservation and also account for their lack of tetrad scars. The relative concentrations suggest an origin within the seed, and none were visible in the matrix external to the integuments. The possibility exists that they might be the functional equivalent of some extant smuts, which replace seed tissue with spores.

Acknowledgment.—The author wishes to express appreciation of the guidance and constructive criticism of Dr. Henry N. Andrews, under whose direction this work was accomplished. For facilities placed at his disposal by the University of Chicago, the University of Cincinnati, the University of Illinois, and the University of Michigan, in the course of this study, the author extends sincere thanks. And particular indebtedness is due Dr. Robert M. Kosanke, of the Illinois Geological Survey, and Mr. Ralph J. Gray, of the United States Geological Survey, Coal Geology Laboratory, for assistance in the spore studies, and to Dr. William G. Chaloner, of the University of Michigan Museum of Paleontology, for his invaluable aid and cooperation.

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EXPLANATION OF PLATE

PLATE 13

Lepidostrobus diversus Felix

Fig. 1. Transverse section of cone through transition zone, showing single megasporangium in spiral of microsporangia. WCB 857 B/3, $\times 6.9$.

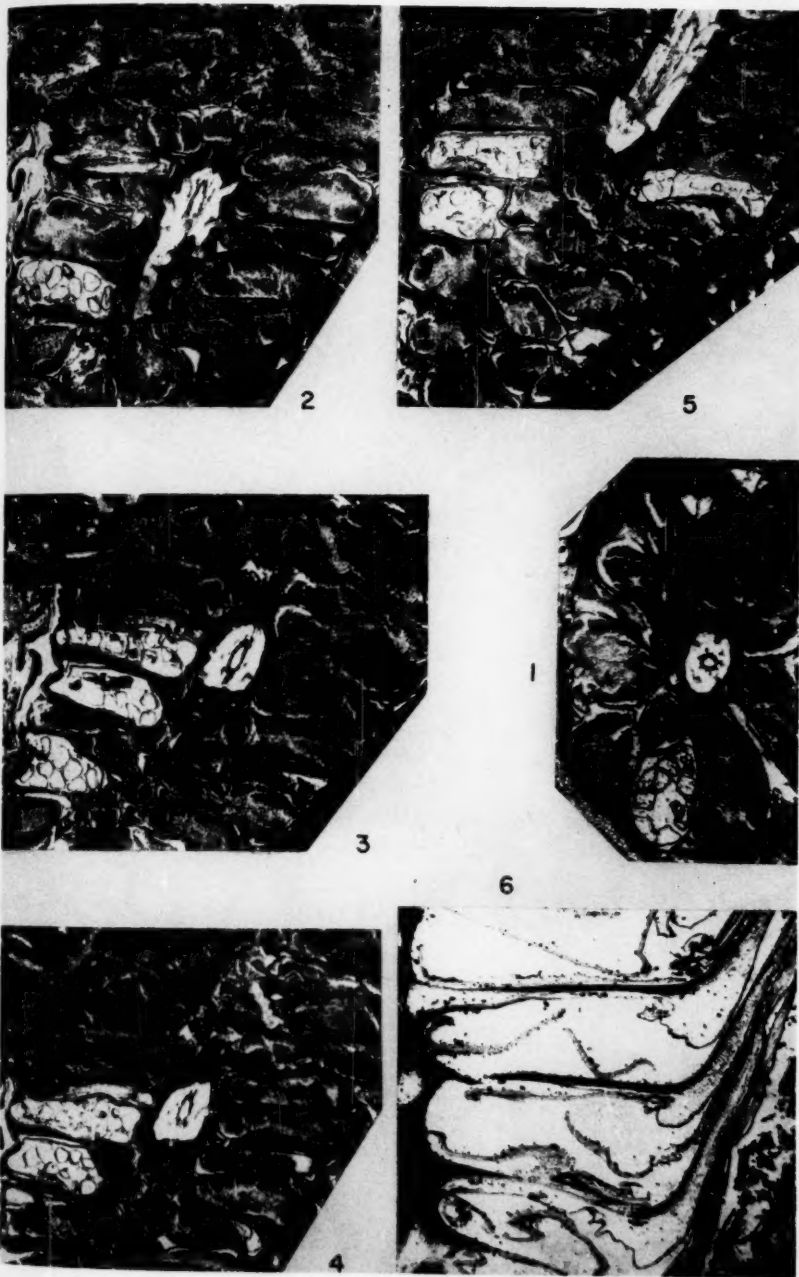
Fig. 2. Slightly oblique longitudinal and transverse sections of transition zone, showing single megasporangium two spirals above one shown in fig. 1. WCB 857 A/5, $\times 5.6$.

Fig. 3. Slightly oblique longitudinal and transverse sections of transition zone with three megasporangia visible. Basal megasporangium is single one visible in fig. 2. WCB 857 A/9, $\times 5.6$.

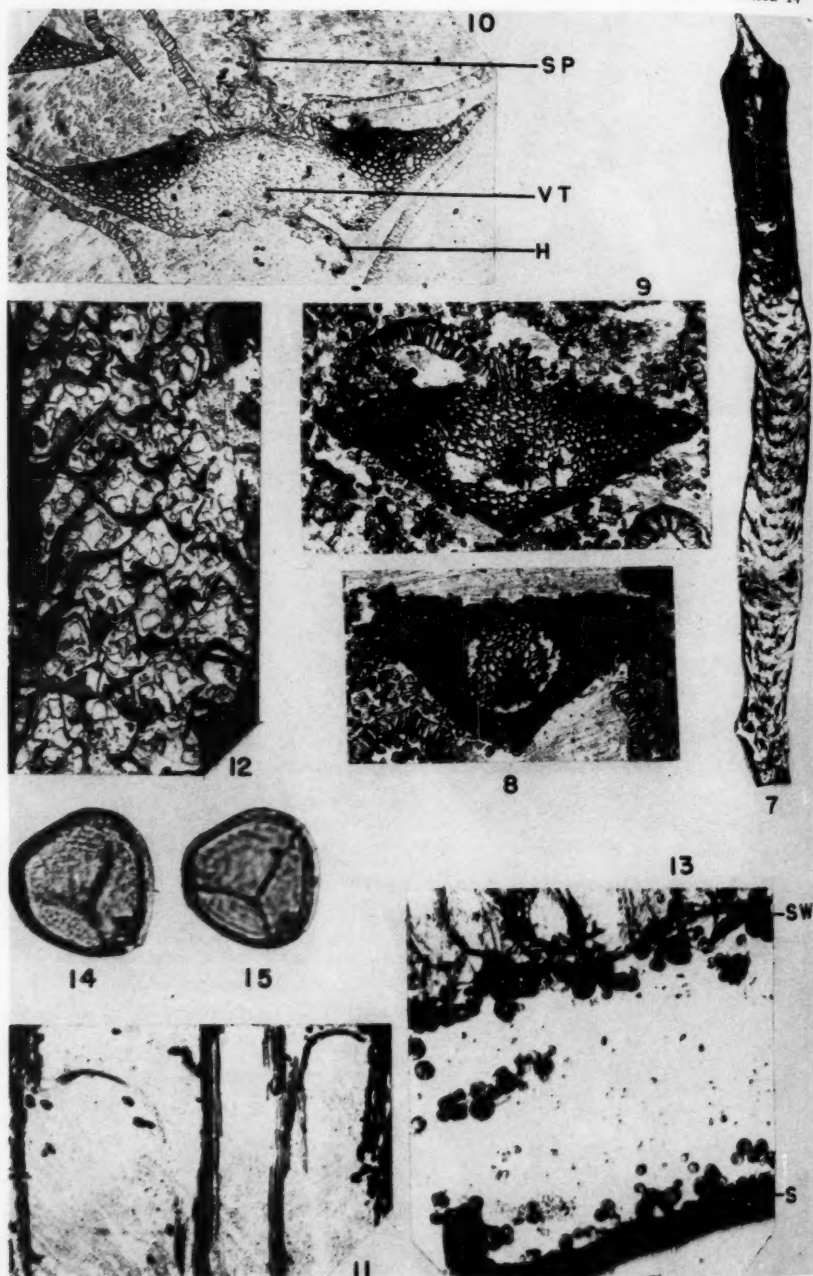
Fig. 4. Oblique longitudinal section of transition zone. Two megasporangia visible are two upper ones of fig. 3, the basal megasporangium of fig. 3 having passed out of the plane of section. WCB 857 A/10, $\times 5.6$.

Fig. 5. Oblique longitudinal section of transition zone, showing new megasporangia appearing on left and right sides of axis. Lower megasporangium on left side of axis is upper one of fig. 4, the lower one having passed out of the plane of section. WCB 857 A/20, $\times 5.6$.

Fig. 6. Radial longitudinal section of sporophylls, showing lobed heel; sporangia have dehisced. WCB 897-1, $\times 11.2$.



FELIX—ARBORESCENT LYCOPOD FRUCTIFICATIONS



FELIX—ARBORESCENT LYCOPOD FRUCTIFICATIONS

EXPLANATION OF PLATE

PLATE 14

Lepidostrobus diversus Felix

Fig. 7. Longisection of cone, showing upper portion containing microspores and lower sporangia dehiscent. Serial peels revealed megasporangia in basal portion. WCB 816 A/5, $\times 1.5$.

Fig. 8. Tangential section of sporophyll pedicel near point of departure from cone axis. WCB 816 A/6, $\times 6.7$.

Fig. 9. Tangential section of sporophyll pedicel midway between cone axis and distal end of sporophyll, showing pedicel wings beginning to form. WCB 816 A/6, $\times 6.7$.

Fig. 10. Tangential section near the distal extremity of a sporophyll, showing widely flared pedicel wings: SP, sterile plate tissue; VT, vascular trace; H, heel. WCB 816 B/T8, $\times 44$.

Fig. 11. Radial section of axis, showing course of sporophyll traces. WCB 897, $\times 35.5$.

Fig. 12. Longisection of portion of cone bearing only megasporangia. WCB 818 B/9, $\times 3.5$.

Fig. 13. Section of megasporangium showing cuticular globules: SW, sporangium wall; S, megaspore wall. WCB 851-2, Slide no. 2257, $\times 415$.

Fig. 14. Proximal view of microspore, showing punctations. WCB 857, Slide no. 2247, $\times 965$.

Fig. 15. Proximal view of microspore of fig. 14 in different focal plane, showing equatorial ridge and trilete rays. WCB 857, Slide no. 2247, $\times 965$.

EXPLANATION OF PLATE

PLATE 15

Lepidostrobos diversus Felix

Fig. 16. Proximal view of microspore, showing width of sutures. WCB 857, Slide no. 2247, $\times 1150$.

Fig. 17. Proximal view of megaspore, showing apical segments and arcuate ridges. WCB 818, Slide no. 2249, $\times 60$.

Fig. 18. Megaspore showing elongate axial dimension. WCB 818, Slide no. 2248, $\times 60$.

Fig. 19. Megaspore showing elongate axial dimension. WCB 818, Slide no. 2248, $\times 63.5$.

Lepidostrobos noei Mathews

Fig. 20. Side view of megaspore, showing spherical shape. Slide no. 2251, $\times 96$.

Fig. 21. View of megaspore of fig. 20, photographed from opposite side. Slide no. 2251, $\times 96$.

Fig. 22. Megaspore of figs. 20 and 21 oriented to show proximal trilete rays. Slide no. 2251, $\times 96$.

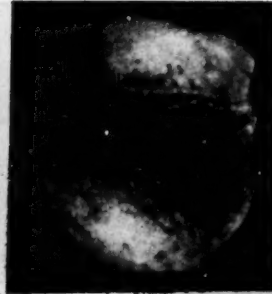
Fig. 23. Cuticular globules attached to coat of megaspores of *L. noei*. Slide no. 2250, $\times 690$.



17



18



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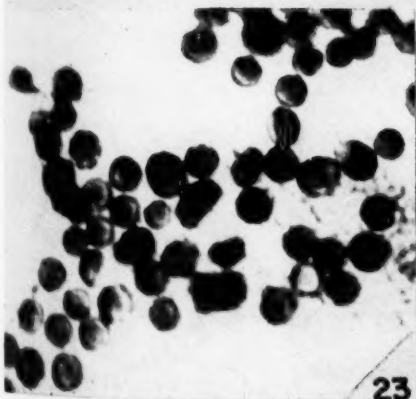
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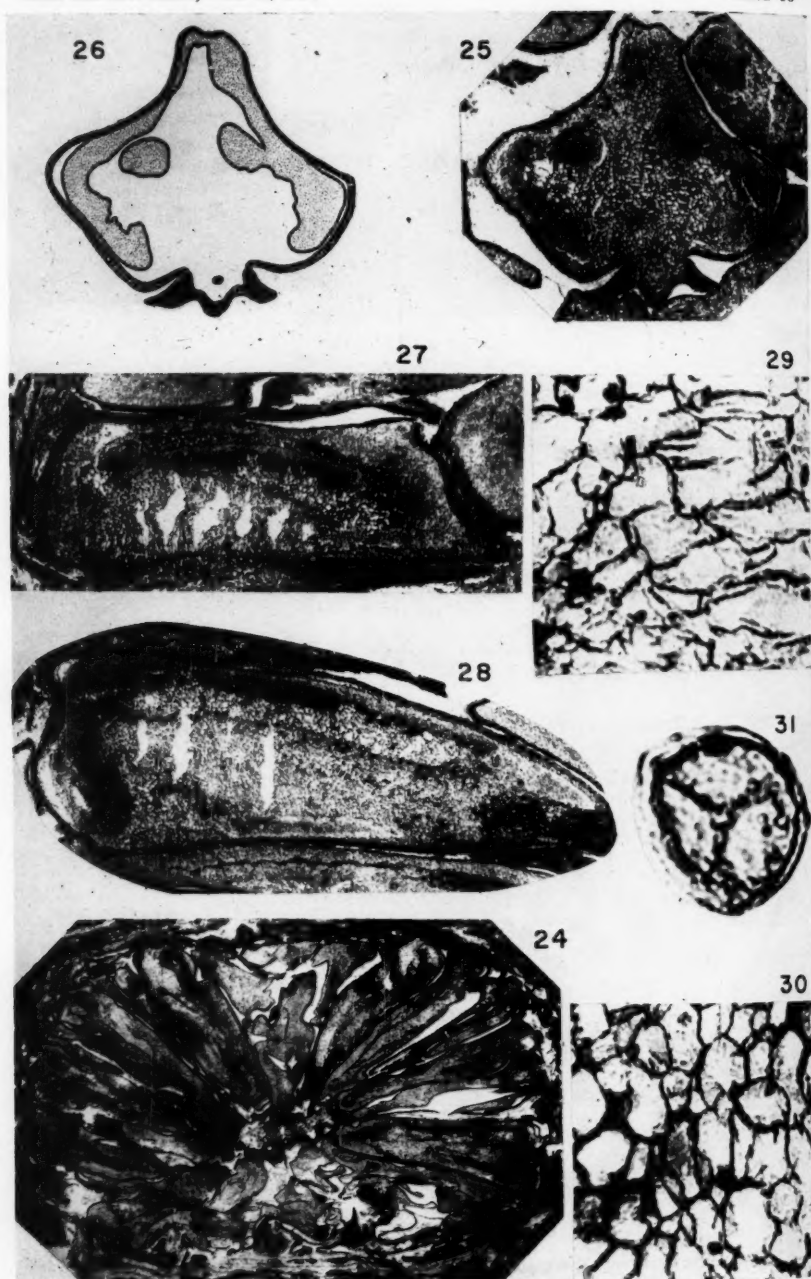


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FELIX—ARBORESCENT LYCOPOD FRUCTIFICATIONS



FELIX—ARBORESCENT LYCOPOD FRUCTIFICATIONS

EXPLANATION OF PLATE

PLATE 16

Lepidostrobus pulvinatus Felix

Fig. 24. Transverse section of cone. WCB 917 B/B10, $\times 2.2$.

Fig. 25. Tangential section of sporangium, showing parenchymatous tissue nearly filling sporangium. WCB 917 C2/S5, $\times 9.5$.

Fig. 26. Diagrammatic sketch of sporangium in fig. 25, showing distribution of spores: stippled portion represents area containing microspores; unstippled portion represents parenchymatous tissue. WCB 917, $\times 9.5$.

Fig. 27. Radial section of sporangium, showing trabeculae. WCB 917 C1/S(2)3, $\times 6.9$.

Fig. 28. Transverse section of sporangium, showing trabeculae. WCB 917 D/T8, $\times 6.2$.

Fig. 29. Basal cells of intrasporangial pad. WCB 917, Slide no. 2268, $\times 90$.

Fig. 30. Cells of intrasporangial pad in upper portion of sporangium. WCB 917, Slide no. 2268, $\times 90$.

Fig. 31. Large microspore which occurred in abundance in basal portion of sporangium. Remnants of a ridge is always evident but preservation is usually poor. WCB 917, Slide no. 2258, $\times 965$.

EXPLANATION OF PLATE

PLATE 17

Lepidostrobos pulvinatus Felix

Figs. 32-45. Spores removed from a single sporangium of *Lepidostrobos pulvinatus*. WCB 917, all magnifications $\times 1360$.

Fig. 32. Distal view of large spore, showing punctations and equatorial ridge. Slide no. 2263.

Fig. 33. Proximal view of large spore without equatorial ridge. Slide no. 2258.

Fig. 34. Proximal view of large spore with equatorial ridge. Slide no. 2263.

Fig. 35. Proximal view of large spore with equatorial ridge. This type composed a high percentage. Slide no. 2263.

Figs. 36-38. Proximal views of medium-sized spores, showing variations in equatorial ridge. Fig. 36, Slide no. 2259; fig. 37, Slide no. 2263; fig. 38, Slide no. 2258.

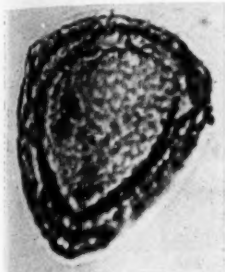
Fig. 39. Proximal view of spore found near top of central pad of tissue, showing brown cuticular bodies on spore coat. Slide no. 2258.

Figs. 40-42. Proximal views of smaller spores found in upper part of the sporangium. Figs. 40, 42, Slide no. 2259; fig. 41, Slide no. 2258.

Fig. 43. Spore tetrad occurring in large numbers in upper part of sporangium. Slide no. 2259.

Fig. 44. Portion of tetrad. Slide no. 2258.

Fig. 45. Large flattened spore, showing punctations. Slide no. 2259.



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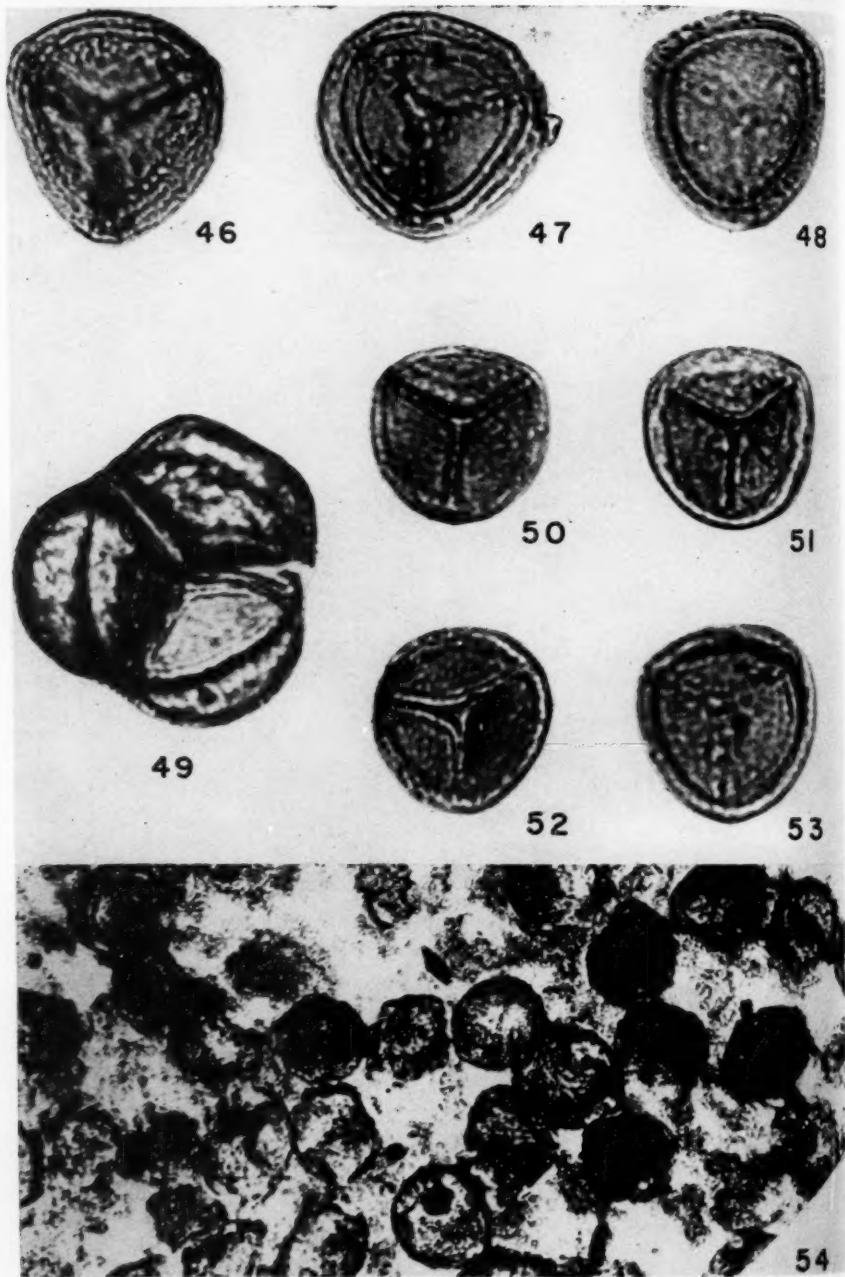


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FELIX—ARBORESCENT LYCOPOD FRUCTIFICATIONS



FELIX—ARBORESCENT LYCOPOD FRUCTIFICATIONS

EXPLANATION OF PLATE

PLATE 18

Lepidocarpon magnificum Andrews & Panne'l

Figs. 46-47. Proximal view of spores, showing ornamentation and ridge characteristics. WCB 166, Slide no. 2316, $\times 1295$.

Fig. 48. Distal view of spore. WCB 166, Slide no. 2316, $\times 1295$.

Lepidocarpon sp. (except fig. 54)

Fig. 49. Spore tetrad, showing equatorial ridges. WCB 847B, Slide no. 2317, $\times 1295$.

Fig. 50. Proximal view of spore, showing punctations and trilete sutures. WCB 847B, Slide no. 2317, $\times 1295$.

Fig. 51. Spore of fig. 50 in different plane of focus, showing equatorial ridge. WCB 847B, Slide no. 2317, $\times 1295$.

Fig. 52. Proximal view of spore. WCB 847B, Slide no. 2317, $\times 1295$.

Fig. 53. Distal view of spore. WCB 847B, Slide no. 2317, $\times 1295$.

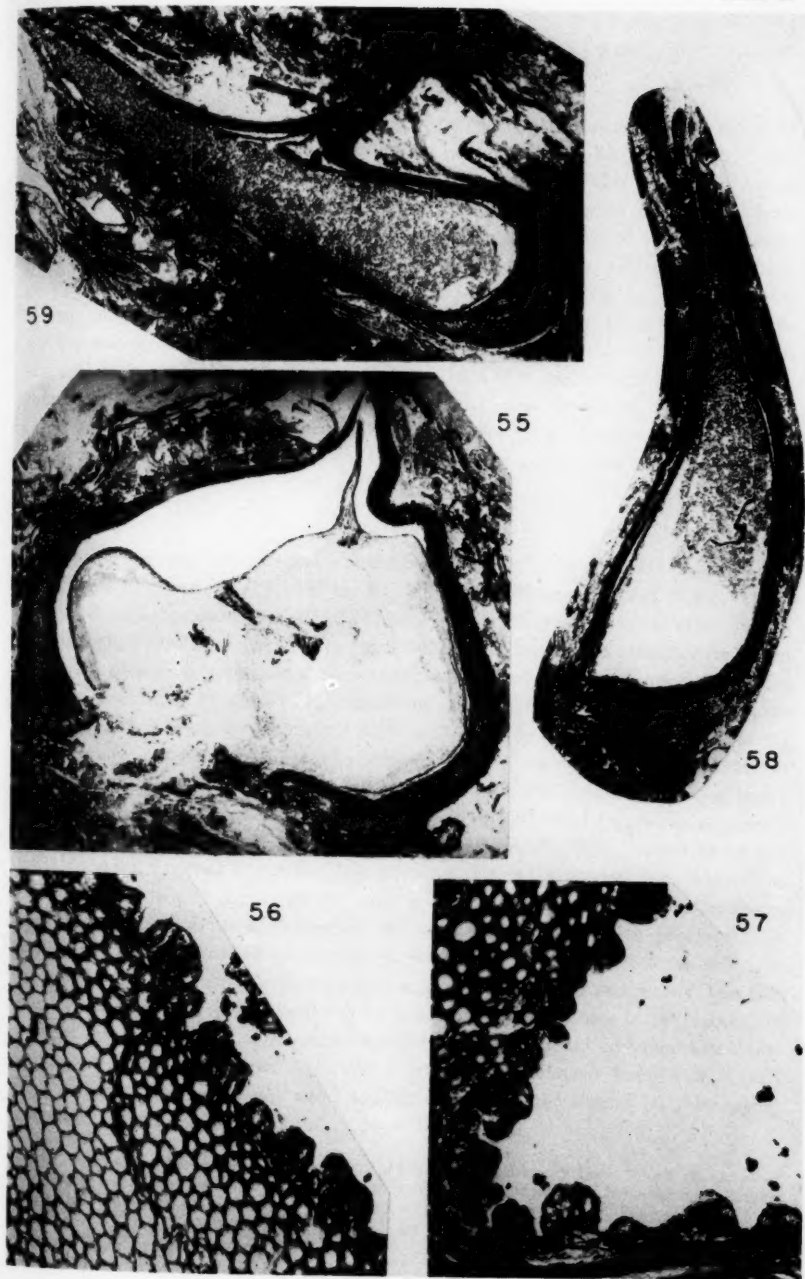
Fig. 54. Fungal-like spores present within lepidocarp seed shown in fig. 59. Slide no. 2255, $\times 260$.

EXPLANATION OF PLATE

PLATE 19

Lepidocarpon crenatum Felix (except figs. 58, 59)

- Fig. 55. Photograph of detached specimen. WCB 816B, $\times 7.6$.
- Fig. 56. Epidermal protuberances near base of specimen. WCB 816B, Slide no. 2252, $\times 82$.
- Fig. 57. Epidermal protuberances of integument near the micropylar opening. WCB 816B, Slide no. 2252, $\times 82$.
- Fig. 58. Integumented lepidocarp, containing probable fungal spores. Slide no. 2254, $\times 8.2$.
- Fig. 59. Integumented lepidocarp, containing probable fungal spores. Slide no. 2255, $\times 7.6$.



FELIX—ARBORESCENT LYCOPOD FRUCTIFICATIONS



A STUDY OF AMERICAN PETRIFIED CALAMITES¹

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The only extensive account of American petrified calamites is that by Andrews (1952), based on a portion of the collection of calamites in his laboratory. Since that time a large number of specimens has been added to this collection which forms the basis for the present investigation. From a study of these it has been possible to determine significant criteria for evaluating species of stem fragments, to record European species as present in American coal balls, and to give definite statistics for established American species. A number of stems fall into two new species, and one fragment is apparently new but too poorly preserved to receive specific assignment. Roots are numerous, and two new species are described. A few coal balls contain an abundance of leaves of a new species sometimes found in connection with twigs. Of special interest is a new species of cone, the first calamitean cone to be described from American coal balls. Finally, a stratigraphic and geographic tabulation is presented based on material within the scope of this investigation.

STEMS

Most of the work on petrified stems has been done by Williamson, Renault and Knoell. Williamson (1871, 1871a, 1878, 1883; Williamson and Scott, 1895, 1895a) described calamites and other fossil plant groups almost strictly from a morphological and anatomical viewpoint. He was loath to found species upon fragments of plants but was not unaware that some variation in stems was specific, and in one instance he did itemize variations of primary rays. Most of the taxonomic work was done by Renault (1885, 1886, 1895-1898) who used a variety of characters to distinguish species. Some characters are sound, such as pitting in tracheids, variation in primary and secondary rays, and orientation of primary tissues; but others, such as internode length based on one small fragment, regularity and frequency of branching, and pith and stem diameter, have proved to be unreliable. Also, varieties of *Arthropitys bistrata* (Cotta) Goeppert were formed on differences that would appear to be clearly specific. Knoell (1935) described some new species and varieties of stems but did not correlate them with previously described species. The use of characters observed chiefly from cross-sectional views is an additional confusing aspect of her work. *Arthropitys communis* was split into two entities, the species and a variety, based upon difference in the manner of primary ray diminution. The species was more closely defined and therefore designated as a new combination, *Arthropitys communis* (Binney) Hirmer & Knoell. This new combination is not valid and the correct name should be *Arthropitys communis* (Binney) Renault.

¹An investigation carried out in the graduate laboratory of the Henry Shaw School of Botany of Washington University, and submitted as a thesis in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

It is apparent from the literature that taxonomy of calamitean stems is inconsistent, and unreliable criteria have sometimes been used to separate species. For purposes of clarification the following is a suggested evaluation of stem characters offered as a guide to the delimitation of species.

I. *Stem Diameter*.—As a distinguishing character this is probably totally unreliable. Only *Arthropityx gigas* (Brongniart) Renault is partially distinct because of its large size.

II. *Internode Length*.—From a study of impression calamites the wide range of internode lengths in one specimen is immediately apparent. In petrified stems it is best to avoid using this feature unless it is constant in several specimens.

III. *Branching*.—This is a major feature in classifying impression calamites. However, unless a petrification is so well preserved that its branching can be correlated with impression types, it has little diagnostic value.

IV. *Pith*.—Whether or not pith is preserved at the periphery and as nodal discs is a matter of age of the stem or fossilization conditions. Pith is the same in all calamitean stems: large, unordered, thin-walled parenchyma. Sometimes dark-colored cells are seen singly or in groups and are of diagnostic value and called resinous cells by some paleobotanists.

V. *Primary Wood*.—Primary wood of each pole is of small amount and borders the protoxylem canal on the outer side. Written description does not serve well to characterize primary wood. Orientation of pith cells about the pole, orientation of tracheids about the protoxylem canal, and relationships with secondary wood—all form a picture varying in each species, and unless illustrated they are of little diagnostic value. Caution is necessary in using the size of the protoxylem canal, for it varies with pith diameter somewhat. This also holds true for the distance between protoxylem poles and width of the fascicular segment. The problem of whether primary wood of the Calamitaceae had endarch or mesarch development has never been resolved, although most authors believe in endarch development for the family. Andrews (1952) described a specimen from Mineral, Kansas, that has a relatively large amount of small, thick-walled cells surrounding the protoxylem canal, giving the appearance of mesarch development. Appropriate radial sections showed no pitting on the cells centripetal to the canal, but this is no disproof of centripetal xylem since preservation is far from good. Despite subsequent collection of a large number of stems from the Kansas locality, none of them are of his "species A" type.

VI. *Fascicular Segment*.—This structure, as a whole, is somewhat stereotyped although its width near the primary wood and rate of widening are specific. Sometimes the segment loses its identity in outer wood due to loss of the primary ray. Tracheid size is constant and of no diagnostic value. Pitting, however, is a fundamental character and is the principal reason for making radial sections of wood. In most calamites the primary tracheids are annular and scalariform, while secondary tracheids may be scalariform, reticulate, or pitted. Usually calamites have one type of pitting in secondary wood or a quick change from scalariform to pitted near the

pith; but rarely a scattered mixture of the three types occurs in one stem. Previous authors have expressed doubt about the diagnostic value of pitting because of this occasional mixture of pitting types and the fact that the interface between tracheids and secondary ray cells is covered with scattered simple pits. Such detail is usually blurred in petrified calamitean stems, and it is difficult to tell simple pits from bordered pits. In any radial section there are likely to be tracheid walls exposed that lie against ray cells. Areas of simple pits so exposed may be found on a tracheid of *Artbropitys communis* known to have scalariform tracheids only. An area free of ray cells should be selected for study of pitting to avoid this difficulty.

Secondary rays may be specific because of their relative frequency, the length of cells, and whether they are simple or compound. Increased frequency and multiseriate conditions in outer wood occur in the same stem; hence, tangential sections from inner wood and outer wood should be made to obtain a true picture of ray conditions. Radial sections show better the height of ray cells.

VII. *Interfascicular Segment or Primary Ray*.—Although synonymy of these two terms is here implied, the primary ray carries a more restricted meaning; in calamite literature it is that part of the interfascicular segment made up of parenchyma.

The interfascicular segment is the most variable tissue in calamite steles and is used as a fundamental diagnostic character. Indeed, generic separation is based largely upon it. It is interesting to note that *Calamodendron* and *Artbroxylon*, with segments composed of prosenchyma flanking primary rays and solid prosenchyma respectively, are specialized. Variation in such segments is so small, even on a theoretical basis, that very few species in these two genera have been described, and it is likely that there will be very few more in the future for this reason. On the other hand, the fact that *Artbropitys* has a large number of species may perhaps be due to the fact that it has an unspecialized segment starting from the pith with a band of homogeneous parenchyma that may vary considerably. Williamson and Scott (1895) outlined the variability of interfascicular segments, which was later refined by Knoell (1935) to include variation of the primary ray in *Artbropitys*. This outline appears as follows.

1. Primary ray persists in secondary wood.
 - a. Primary ray remains constant in width.
 - b. Primary ray gradually becomes narrow.
2. Primary ray does not persist in secondary wood.
 - c. Primary ray disappears abruptly with onset of cambial activity.
 - d. Primary ray disappears somewhere in secondary wood.
 - (1) Proportion of ray parenchyma in interfascicular wood then becomes equal to that in fascicular wood.
 - (2) Proportion of ray parenchyma in interfascicular wood becomes greater than that in fascicular wood.

Of interest are the several ways by which rays diminish or disappear within secondary wood. They have been summarized in essence by Knoell as follows:

1. Tapering due to decrease in cell size or cell row number.
2. Tapering due to insertion of new tracheid rows at margin.
3. Tapering due to replacement of ray cells by tracheids in flanking rows.
4. Disintegration due to insertion of new tracheid rows between median rows.
5. Disintegration due to replacement of ray cells by tracheids in median rows.

One or more of these factors operate in any species and should be noted in a description.

Tangential sections show best the vertical extension of primary ray cells, which is of diagnostic value. Also supra- and infra-nodal canals appear in this view as swellings at each end of a ray. When tissue is present, it is irregular, isometric parenchyma. The infra-nodal canal is the larger of the two, making it possible to orient the direction of the axis. In some stem species canals are not prominent, but in others they persist as hollow structures even after the primary ray has disappeared, and are real "canals."

The bulk of the collection used in this investigation consisted of some 70 odd stem fragments. Most of them are from three localities: West Mineral, Kansas; Berryville, Illinois; and Booneville, Indiana. A few specimens are from several localities in Iowa, Illinois, and Indiana. Most specimens belong to the genus *Arthropitys*. There are several specimens of *Arthroxylon*, chiefly from Iowa, but none of *Calamodendron*. A few specimens fall into species of European material and a considerable number into American species already described.

ARTHROPITYS illinoensis Anderson, sp. nov.

This species is based on eight specimens collected from Berryville, Nashville, Freeburg, and Dix, Illinois. All stems are decorticated and are of three size classes. Three are hardly more than twigs, with pith diameters ranging from .6 to 1.1 cm. and total diameters from .9 to 1.4 cm. Four are intermediate with pith cavities and total diameters varying from 2.2 to 3.0 cm. and 4.1 to 6.5 cm., respectively. The largest stem is unusual in that its pith (diameter 6.5 cm.) is surrounded by a sheath of secondary wood only .5 cm. thick. It is apparently the remains of a young major axis fossilized before much secondary wood had formed and presumably before the axis had elongated much beyond this level.

Cross-sectional views (pl. 20, fig. 3) show that pith tissue is preserved between fascicular segments only. The segments themselves are wide, spaced nearly 2 mm. apart, and characteristically blunt at the inner edge. Circular protoxylem canals are relatively large, ranging from 175 to 250 μ in diameter. The primary ray disappears quickly, its parenchymatous cells being replaced by tracheids soon after initiation of cambial activity. Fascicular segments merge into a homogeneous sheath of secondary wood interspersed with secondary rays. A tangential section cut fairly near the pith (fig. 7) shows alternate wood sectors and primary rays. Ray cells are elongate vertically and may reach 300 μ in height. Near the nodes rays enlarge at both ends into the nodal canals formed of irregularly packed, isometric cells. Within an internode secondary rays are sparse and hard to see because

they are uniseriate and composed of elongate cells, 100–300 μ tall, separated by slanting cross walls. Within a nodal region secondary rays are numerous and multi-seriate. Figure 5 is a radial section showing rays cut in various sections. Here the elongation of ray cells is more apparent. Tracheids have three to four rows of alternate bordered pits.

The type specimen is of special interest since there are three roots attached to it which appear to be referable to *Astromyelon Williamsonis* (Cash and Hick) Williamson. These decorticated roots are about 1.5 cm. across. Broad, blunt, fascicular segments with prominent central secondary rays, large centripetal tracheids, uniform fascicular and interfascicular wood, so characteristic of *A. Williamsonis*, are easily observed. The segments originate from the innermost wood of the stem and at the same level as leaf traces. The pith cavity enlarges gradually in its outward course, and toward the inside there seem to be peripheral "canals" which are really small groups of large, thin-walled cells, giving the root primordium a stem-like appearance; they disappear farther out. The course of the root is perpendicular to the stem axis for about 1 cm.; then it gradually bends downward at a 30 degree angle upon emerging from the stem stele.

Diagnosis.—Decorticated stem 1–6.5 cm. in diameter, and internodes 1– several cm. long; pith cells usually absent; primary wood scarce, partially bordering a circular protoxylem canal 175–250 μ across; fascicular segment blunt at inner edge, broad and merging with others due to rapid loss of primary ray; tracheids with several rows of alternate oval pits; secondary rays sparse, uniseriate with elongate cells up to 300 μ tall, except at nodes where they are copious, multiseriate, and short-celled.

Type specimen: Coal ball no. 947, Henry Shaw School of Botany, Washington University, St. Louis, Missouri.

Locality, horizon and age: Berryville, Illinois; Calhoun coal, upper McLeansboro group; Upper Pennsylvanian.

Other specimens and localities:

1. Coal ball nos. 860c, 948, 949, 950; Berryville, Illinois.
2. Coal ball no. 951; Freeburg, Illinois.
3. Coal ball no. 952; Nashville, Illinois.
4. Coal ball no. 953; Dix, Illinois.

ARTHROPITYS versifoveata Anderson, sp. nov.

Arthropitys sp. B. Andrews, in Ann. Mo. Bot. Gard. 39:189–218. 1952.

Andrews reported briefly on a large *Arthropitys* stem fragment from West Mineral, Kansas. Its poor preservation prevented a full description, and no specific name was assigned. Since then at least eight additional specimens of this stem have been collected from the Mineral locality, making possible a definite erection of a new species.

All the stems are decorticated and probably fragments from a major axis if not the primary axis, for their pith diameters range from 2.5 to 7.5 cm. and total

diameters from 5 to 9 cm. Internodes vary with stem diameter and range from 1.2 to 3 cm. Of exceptional interest is the smallest stem (no. 956) which projects several centimeters beyond the end of the coal ball imbedding it, showing its nodes and branching habit. Nodes are spaced 1.2 cm. apart and each bears four branches 4 mm. thick and 90 degrees apart. Branches of one node alternate with those of adjacent nodes. That these structures are branches and not roots is proved by a tangential section showing them to arise somewhat above the level of leaf traces, as is characteristic of calamitean branches. It is therefore possible to place this species in the *Cruciatius* subgroup of the *Eucalamites* group of impression species.

Most of the pith is lost although it persists at the periphery and as pith disc remnants at nodes. Protoxylem canals are circular, varying from 150 to 200 μ across and are surrounded on three sides by primary tracheids (fig. 6). Each fascicular segment enlarges rapidly by insertion of new tracheid rows at the margin; thereafter it broadens very slowly toward the outside. Rather infrequently new rows of tracheids are inserted at the margin or middle of the ray, narrowing it or cutting it into two or more parts. In tangential section primary ray cells are nearly isometric, being elongated toward the margin (fig. 4).

Secondary tracheids have either scalariform or reticulate-bordered pitting (figs. 9 and 10). Both types are scattered at random throughout a stele and the proportion of each varies considerably among stems. So, while variation in proportion of pitting type is individual, the presence of this curious mixture is characteristic to this species along with a number of other features that are more constant. Secondary rays are made up of cells up to 200 μ tall. Rays are strictly uniseriate near the pith but may be biseriate farther out. Within nodal regions wood rays become more frequent and thicker.

This species is much like *A. kansana* Andrews with which it is usually found. Smaller primary wood groups, lack of strictly bordered pitting of tracheids or prominent biseriate rays are the chief characters that set it off from *A. kansana*.

Diagnosis.—Decorticated stem 5–9 cm. in diameter with internodes 1.2 to 3 cm. long; branches at every node alternating with those at adjacent nodes; protoxylem canal 150–200 μ across, surrounded on three sides by a relatively large amount of metaxylem; fascicular segment blunt, broadening very slowly and remaining distinct in outer wood; primary ray persisting as a band 4–6 cells wide, occasionally narrowed or split by insertion of new tracheid rows at margin or center; tracheids with scalariform or reticulate bordered pitting, both types scattered irregularly throughout the stem and in different proportions among stems; secondary rays of cells up to 200 μ high, uniseriate and sparsely biseriate in outer wood.

Type specimen: coal ball no. 829, Henry Shaw School of Botany, Washington University, St. Louis, Missouri.

Locality, horizon and age: West Mineral, Kansas; Fleming coal, upper Cherokee shale, Des Moines series; Middle Pennsylvanian.

Other specimens and locality: Coal ball nos. 754, 788, 826, 828, 954, 955, 956; West Mineral, Kansas.

ARTHROPITYS SP.

The following description is based upon a fragmentary specimen (coal ball no. 957) from New Delta, Illinois. Although it appears to be a new species it will not be given a species assignment because of its poor preservation and fragmentary condition. Only a sector of the stele is preserved showing a small part of the pith cavity surrounded by 2 cm. of secondary wood. Protoxylem canals are about 200 μ across and appear to abut directly onto the secondary wood. The fascicular segment is relatively narrow, ranging from .5 to 1.0 mm. passing toward the outermost secondary wood. The primary ray is about six cells wide and persists undiminished in the secondary wood (fig. 12). Secondary rays are uniseriate near the pith but farther out they are multiseriate and may be nearly as large as primary rays, giving the wood a somewhat uniform appearance in tangential view (fig. 8). Tracheids have three or four rows of circular pits on the radial walls. With its uniform primary ray and small pith cavity relative to thickness of secondary wood, this species resembles *A. bistriata*, but tracheids are pitted instead of scalariform as in this European species.

OTHER STEMS

There are two large stems (nos. 772 and 937) of *Arthropitys communis* from West Mineral, Kansas, that are very typical, with blunt, narrow fascicular segments, small protoxylem canals, scalariform tracheids and diminishing primary rays. Another specimen (no. 932) of this species is from Atlas Mine near Oskaloosa, Iowa. It is rather badly preserved, and this determination is tentative.

From Berryville, Illinois, several more specimens of *A. communis* var. *septata* Andrews have been collected (nos. 938-943), all of them remarkably alike, especially with 6-8 mm. internodes and septate tracheids of inner secondary wood. The status of this variety is more certain, because these characters which might seem questionable stand up statistically. Indeed, it can be suggested that this variety deserves specific status.

In a coal ball (no. 841) from Booneville, Indiana, there is a calamite stele with 9 cm. of secondary wood. Since only a sector of the stele is preserved, pith diameter is estimated to be 12 cm. From tangential sections it is seen that primary rays split into short, overlapping, multiseriate rays only slightly larger in outer wood than secondary rays, which also become multiseriate in outer wood. In the outermost wood there is a very high proportion of ray tissue and relatively few tracheids. Tracheids have alternate oval pits on their radial walls. By its size and anatomy this specimen is assigned to *Arthropitys gigas*.

Arthropitys Hirmeri Knoell is represented in a coal ball from Pinckneyville, Illinois (no. 568). It is a small stem with little secondary wood and has the characteristically abrupt loss of the primary rays immediately upon initiation of secondary growth.

From West Mineral, Kansas, there are six stems identified as *Arthropitys kansana* (nos. 750, 787, 789, 791, 830, 944). Also most stems (nos. 837, 838, 839, 840,

844, 877, 945) from Booneville, Indiana, are undoubtedly *A. kansana* despite the fact that their aspect is slightly different from the Kansas specimens. Upon careful comparison it is found that every character of the Booneville stems matches that of the West Mineral stems: general size, orientation of primary wood with pith and fascicular segments, protoxylem canal size of $250\ \mu$, very slow diminution of the primary ray which is made up of small isometric cells, presence of biseriate rays in secondary wood, and several rows of alternate bordered pits on radial walls of tracheids. Their slightly different aspect is interpreted as an outcome of general difference in preservation of material between the two localities.

There is one Booneville specimen (no. 875) very similar to *A. kansana*, but it has scalariform pits on tracheids and ray cells tend to be elongated. The primary ray does not appear to diminish in the small amount of secondary wood present. This stem is tentatively assigned to *A. bistriata*.

Artbroxylon Williamsonii Reed is represented by three small stems, one (no. B-13) from Oskaloosa, Iowa, and the other two (nos. 933 and 936) from What Cheer, Iowa. A fourth stem (no. 946) comes from West Mineral, Kansas, and is unlike all stems previously described because of its large size. Pith diameter is 7.3 cm. and secondary wood is 2.3 cm. thick. It is identical with the *Artbroxylon* stem briefly reported by Andrews (1952). Like most West Mineral calamites it is fusainized from the pith cavity outward and highly pyritized from the outside in. Between pyritized and fusainized zones there is a small neutral band, the only hope for good study, suggesting that factors promoting formation of the two conditions are opposing and each tends to prevent the other from occurring. Primary wood and protoxylem canals can be seen, however, and are like those of *A. Williamsonii*; this specimen is probably a primary axis of this species. A tangential section through the well-preserved zone, cut about 1 cm. from the pith (fig. 13), shows that the fibrous zone does not contrast as sharply with the fascicular segment as in smaller stems. Another difference is the presence of a larger proportion of short-celled secondary rays, even in the fibrous zone, where they are absent in smaller stems. Such increase of ray parenchyma is probably in accordance with Bower's "size and form" principle and does not represent specific difference.

TWIGS AND LEAVES

Calamitean twigs are seldom found in coal balls although they are found as impressions in abundance. Williamson described some petrified twigs, and Hick (1894) gave a full treatment of them, noting their very close similarity to stems of *Equisetum*. Andrews (1952) briefly described two twig specimens probably identical to those described below. Isolated leaves are also infrequently found. Hick (1895) wrote a short account of them, but a more comprehensive treatment was made by Thomas (1911) who brought together scattered information about leaves and designated several specific types. In America only Hoskins (1928) and Reed (1938) have described petrified calamitean leaves.

In the present study the smallest stems found range from .7 to 3.0 mm. in diameter, forming a size class distinct from another class which ranges from 6 to 10 mm. The smaller class will be termed twigs in this paper, and the larger small stems. Only the twigs are definitely assigned to the new species erected below.

CALAMITES rectangularis Anderson, sp. nov.

This species is based on a large assemblage of shoots, isolated twigs and leaves in three coal balls from Berryville, Illinois.

In considering twig size, the diameter of the primary body (including distance across the pith plus primary wood) is more informative than total twig diameter. Since the cortex is somewhat uniform in thickness, complications of including secondary wood are thereby avoided and errors in measurement due to loss of phloem in preservation are minimized. Also, the distinction between twigs and stems is more apparent when the diameter of the primary body is used rather than total stem diameters. The primary bodies of 58 twigs measured varied from .2 to 1.0 mm. in diameter, with a median and mode of .6 mm. This variation shows a normal distribution; hence these twigs represent the highest order or ultimate branches of a calamite. The measurements show that these coal balls happened to preserve an ultimate branch system that is often preserved intact in an impression. For comparison, an impression of *Asterophyllites charaeformis* Sterenberg, taken at random, shows the last three degrees of branching. The largest axis is fragmentary and measures 4 mm. in diameter. The secondary axes are 1.5 mm. across at the base and .5 mm. near the tip, and the ultimate axes are .2 to .4 mm. across. The smallest part of the secondary axis is about as large as the largest ultimate branches, so it is possible that the fragments in the coal balls may represent two degrees of branching instead of one.

Leaves measure .3–.5 mm. in thickness, .5–.7 mm. in width, and 5–10 mm. in length. Thirteen leaves per whorl may be counted in one specimen (fig. 14), and other shoots appear to have about 12 per whorl. Variation in leaf size seems to be comparable to that in twig size. Figure 16 shows a representative longitudinal view of a shoot.

The anatomy of a twig is typically calamitean, with a ring of fascicular segments, each with a protoxylem canal, unpreserved phloem, and primary cortex of two layers. The smallest twig is .6 mm. in diameter with a primary body .2 mm. thick. There are five fascicular segments and no secondary wood. A better-preserved specimen, shown in fig. 20, is slightly larger and 1 mm. in diameter; the primary body is .4 mm. thick, and has seven fascicular segments. The cortex is intact and there appear to be about twelve leaves per whorl. Twigs with a primary body approaching 1 mm. in diameter have 12 to 20 fascicular segments and may have up to .2 mm. of secondary wood (fig. 19). Otherwise they are quite similar to the smallest twigs.

As stated above, leaves seem to vary with their twigs in size. However, the larger leaves form a distinct class, sometimes being 1.5 × .8 mm. in cross-section

but found closely associated with small stems about 6 mm. in diameter. Figure 15 shows cross-sections of leaves of both size classes that happen to be adjacent. The larger leaf is $1.5 \times .6$ mm. and the smaller is $.7 \times .4$ mm. They are oriented in the same direction. Their cross-sectional shape is almost perfectly rectangular, quite unlike that of leaves previously described. There is a single layer of epidermis present, with some poorly defined stomata on the lower surface of the larger leaf. A palisade layer next underlies the surface and extends nearly around the central tissues. At the center there is a single strand of perhaps 20 tracheids. Phloem cells are probably not preserved. Surrounding the stele is the bundle sheath, which is proportionally larger than that in other species. Next to the stele, cells of the sheath are large and very thin-walled. Toward the outside they are smaller with thicker walls, and in longisectional view they appear fibrous. This fibrous zone is more pronounced on the upper side where it seems to form a sort of backbone for the leaf.

Diagnosis.—Shoot .7–3.0 mm. in diameter, bearing 12 leaves in whorls 1–5 mm. apart; axis calamitean with ring of fascicular segments each with a protoxylem canal and 2-layered cortex; leaves 5–10 mm. long and $.3 \times .5$ to $.8 \times 1.5$ mm. and of rectangular shape in cross-section, palisade layer and large bundle sheath surrounding single, unbranched vascular strand.

Type specimen: Coal ball no. 834, Henry Shaw School of Botany, Washington University, St. Louis, Missouri.

Locality, horizon and age: Berryville, Illinois; Calhoun coal, upper McLeansboro group; Upper Pennsylvanian.

Other specimens and locality: Coal ball nos. 860, 879, 960; Berryville, Illinois.

The larger stem-size class ranges from 6 to 10 mm. in total width. Apart from being larger than twigs their organization is different. Primary wood groups and protoxylem canals are larger and more spaced out. Secondary wood is always present. Figure 18 shows a small stem about 6 mm. thick. There are 24 fascicular segments and .1 mm. of secondary wood. It seems evident, from comparing this stem with twigs one-fourth as large but with about the same number of fascicular segments, that the two represent different orders of branching. It is inconceivable that a twig could expand its width fourfold to become a small stem such as is figured. From this specimen and others scattered throughout the coal balls there can be seen a stelar organization similar to that of *Arthropitys illinoensis*. Configuration of the primary body and quick loss of the primary ray are partial evidence that the specimens belong to this species. It is further suggested that the twigs and leaves described above also belong to this stem species because of their close association with these small stems.

ROOTS

Petrified calamitean roots were first described in 1878 by Williamson, who assigned them the generic name *Astromylon*. He found isolated fragments only and suspected that they might be stems somewhat allied to calamites. It remained

for Renault and Zeiller (1890) to find them in organic connection with calamitean stems, confirming Renault's earlier hypothesis that they were roots of calamites. Renault also designated four of the five species of *Astromylon* so far described. Anatomical descriptions were given by Renault, and by Williamson and Scott (1895a). Maslen (1905) wrote a masterly discussion of root-stem relationships.

During the present investigation isolated roots of various size were found, ranging from 2 mm. to several cm. in diameter. Although at least three size classes are represented, no very small roots have been observed of the type formerly called *Myriophylloides* with diarch or tetrarch protosteles and cortex with large intercellular spaces. In fact, no extra-xylary tissues were preserved in any roots observed. This assemblage appears rather varied anatomically, but some instances of branching make it possible to designate a small number of types.

Coal balls (nos. 840, 870, 872, 878, 947, 958) from Booneville and St. Wendells, Indiana, and Berryville, Illinois, were found to contain calamitean roots belonging to *Astromylon Williamsonis*. The somewhat indistinct fascicular segments projecting only a little into the pith, quick replacement of interfascicular parenchyma by tracheids, a prominent secondary ray in the middle of each fascicular segment, and very large, thin-walled centripetal tracheids are characters that check point for point with described and illustrated specimens of this species from European coal balls. Such distinct characters are present only in root steles ranging from 4 to 10 mm. in diameter, roots of an intermediate order of branching. Associated steles of smaller size appear somewhat nondescript and similar to roots of this size belonging to other species.

ASTROMYLON cauloides Anderson, sp. nov.

This species is based on a number of roots found in coal balls from Berryville, Illinois, and St. Wendells, Indiana. All specimens are decorticated and their steles range from 2 mm. to several cm. in diameter, with a common anatomical configuration in all sizes except the very smallest which are nondescript.

The most characteristic features of this species in cross-sectional view are the rather pointed fascicular wedges accentuated by the presence of considerable interfascicular parenchyma. In a segment, centripetal metaxylem is reasonably well-developed and projects into the nearly intact pith, giving a distinct point to a segment. Wood rays are mostly uniseriate. The primary ray is lost through replacement of parenchymatous cells by tracheids in a radial row of cells plus the insertion of new rows of tracheids. There is considerable variation in the rate of ray loss; smaller roots and some larger ones lose their primary rays almost as soon as production of secondary wood begins (fig. 17), while in others the ray persists through 4 mm. of secondary wood (fig. 1). The writer does not believe that such variation constitutes specific difference, since all other characters are constant, especially the manner of ray loss, and there is a continuous series of ray-loss rates among the observed specimens.

This root most closely resembles *Astromyelon augustodunense* Renault, in which the primary ray persists considerably into secondary wood. In this species, however, ray loss is accomplished by a decrease in ray row number only. There is no replacement of parenchymatous cells by tracheids, and the outer tracheidal row of a fascicular segment flanking a ray in the inner wood remains as the flanking row until it meets, in outer secondary wood, a flanking tracheidal row of the next segment. Figure 2 is a tangential section near the pith showing primary rays and wood sectors. Cells of primary rays are large and somewhat elongate ($75\text{--}300\ \mu$), as well as those in the uniseriate secondary rays scattered among tracheids. Pitting on radial walls of tracheids is strictly scalariform.

In its anatomical organization this root appears more like a stem than the other root species. It is further suggested that it belongs to *Arthropitys communis* var. *septata* on the basis of association in coal balls and such anatomical details as elongate ray cells and scalariform pitting.

Diagnosis.—Decorticated root 2–40 mm. in diameter; pith nearly intact and of thin-walled parenchyma; primary xylem mesarch with protoxylem poles at periphery of pith, no protoxylem canals present; secondary fascicular wood with scalariform tracheids and 1–2 seriate rays 2 to many cells deep; ray cells up to $300\ \mu$ deep; interfascicular segment with a varying amount of primary ray lost through replacement of parenchymatous cells by tracheids in a given row plus insertion of new tracheid rows.

Type specimen: Coal ball no. 853, Henry Shaw School of Botany, Washington University, St. Louis, Missouri.

Locality, horizon and age: Berryville, Illinois; Calhoun coal, upper McLeansboro group; Upper Pennsylvanian.

Other specimens and localities:

1. Coal ball nos. 882, 887, 929, 930, 931; Berryville, Illinois.
2. Coal ball nos. 925, 926, 927; St. Wendells, Indiana.

ASTROMYELON pluriradiatum Anderson, sp. nov.

This species is based upon a single specimen in a coal ball from Berryville, Illinois. It most closely resembles *Astromyelon reticulatum* Renault, which is figured showing very broad fascicular segments similar to those in this new root. However, the small amount of secondary wood in Renault's specimen makes precise comparison impossible. The stele is decorticated, the pith cavity is 6 mm. in diameter, and there are 7 mm. of secondary wood. Figure 21 shows a cross-section that happens to cut a branch root in its outward course; outside the main axis it has a diameter of 1 cm. and organization similar to that of the parent root.

The chief characteristic of this root is its high proportion of ray tissue in secondary wood. This is apparent even in cross-section where a very prominent 3- to 4-seriate ray appears centrally in each fascicular segment. In tangential view the high proportion of ray parenchyma (fig. 11) makes the wood appear almost herbaceous. Rays are 1- to 4-seriate and the largest may be over 1 cm. deep.

Multi-seriate rays form an overlapping network of parenchymatous tissue in the center of a fascicular segment, a condition opposite to that in calamitean stems and most roots where the interfascicular segment is more parenchymatous. Ray cells are little elongated, being rather isometric in multiseriate rays; their depth ranges from 50 to 150 μ .

The pith cavity is nearly hollow with tissue only at the periphery. Fascicular segments are very broad and blunt due to a small amount of primary wood, immediate succession of secondary growth, and rapid insertion of new tracheidal rows in each segment. A radial section through a protoxylem pole shows annular tracheids of protoxylem and a few scalariform tracheids of centrifugal metaxylem. Cells of the centripetal xylem are pitted and seem to be transitional to parenchyma, for they are shorter, have thinner walls and squared end-walls. Secondary tracheids have either single rows of elongate pits or 3-4 rows of alternating oval pits and are up to $50 \times 60 \mu$ in cross-section. Primary rays lose their identity quickly through rapid tapering and replacement of parenchymatous cells by tracheids in any given cell row.

Diagnosis.—Decorticated root 2 cm. in diameter with connected branch root 1 cm. thick; pith 6 mm. across, hollow, with peripheral parenchyma only; primary xylem mesarch with 12 protoxylem poles at periphery of pith; centripetal metaxylem of thin-walled, short, square-ended tracheids; fascicular segments very broad and blunt facing the pith; secondary wood with high proportion of ray parenchyma, especially in center of fascicular segment where there are up to 4-seriate rays; ray cells 50-150 μ deep; secondary tracheids to $50 \times 60 \mu$ in cross-section with single rows of elongate pits or several rows of alternate oval pits; primary ray lost through replacement of parenchymatous cells by tracheids in a given radial row of cells.

Type specimen: Coal ball no. 959, Henry Shaw School of Botany, Washington University, St. Louis, Missouri.

Locality, horizon and age: Berryville, Illinois; Calhoun coal, upper McLeansboro group; Upper Pennsylvanian.

CONES

In the thirty-odd years in which coal balls have been cut and studied in America, calamitean cones have very rarely been discovered in them. Some of the earlier workers listed their occasional presence, but to date there have been no descriptions of them, although several paleobotanists are currently working on such cones and papers should be soon forthcoming. The present investigation covers nine cone specimens, eight of which belong to one species. All of them are assignable to *Palaeostachya* owing to adaxial insertion of sporangiophores. One of the cones is about 2 cm. in diameter while another is at least 3 cm. in diameter. None of the *Palaeostachya* species described from petrifications comes close to approaching this size, and, of impression species, only *P. arborescens* Sternberg and *P. Schimperiana* Weiss are in this size class, being 3 and 2.5 cm. in diameter respectively (Weiss,

1876, 1884). Correlation of these impression species with the new petrified cones is ruled out, since *P. arborescens* has about 20 bracts per whorl while the corresponding petrified cone has from 40 to 60; and *P. Schimperiana* has an axis 1 cm. thick while the petrified cone has one about 4 mm. thick.

PALAEOSTACHYA multifolia (Reed) Anderson, comb. nov.

Calamites multifolia Reed, in Bot. Gaz. 100:324-335. 1938.

This species is based upon six specimens in coal balls from Berryville, Illinois, and two in a single coal ball from Booneville, Indiana. The complete cone is at least 8 cm. long and 3 cm. wide. Toward the base it narrows to 1.5 cm., the tapered zone being sterile. Nodes are spaced 3 to 4 mm. apart and bear 40-60 whorled leaves fused at their bases. Sporangiphores arise obliquely from bract axils and bear four pendant sporangia. This species is heterosporous.

At the very base the axis is small and consists of xylem only. The primary body is 2 mm. in diameter and secondary wood is .5 mm. thick making the total diameter 3 mm. In cross-section it is perhaps indistinguishable from a stele of a vegetative twig (fig. 22). A few scattered bracts are present at this level. The stele then enlarges to its full width of 6 mm. in a distance of 2 cm. A cross-sectional view of the widened axis shows a somewhat different organization than that below. The stele is crushed to an elliptical shape, and loosely surrounding cortex is present. There are now 26 fascicular segments in contrast to 18 at the level below. Segments show a tendency to group into pairs and there are .3 mm. of secondary wood. The uppermost cross-section of the axis shows it to be the same size, but with very little secondary wood, and a very pronounced tendency for the segments to group in pairs (fig. 24). There are now 30 fascicular segments. Since there is very little secondary wood at this level, the cone probably does not extend much farther. A tangential section through the stele gives proof that bracts of one whorl are superposed on those of the whorl below. At most nodes fascicular segments of the internodes above and below stand directly in line with each other. Only a few show alternation at nodes, marking the insertion of new segments into the stele. Hence, most leaf traces and their bracts arise directly above each other.

The bracts of a whorl number from 40 to 60 in the widest part of the cone and are fused basally into a lateral disc. This disc is very well shown in the specimen from coal ball no. 858 (fig. 25). When a small piece of the cone was accidentally broken off, the top surface of a whorl of fused bracts was exposed. One-fourth of the whorl contains 10 bracts, so the whorl must contain 40. This whorl is near the base of the cone and does not have the maximum number of bracts possible. From the photograph it can be seen that the bracts are fused into a basin-like disc, with the mid-portion of each bract ridged somewhat. The disc dips down a little before bending up sharply to a rim where the bracts separate. Cells composing the disc are rather elongate with walls of moderate thickness. This tissue persists into the upturned free bract, forming a sort of "backbone" which gradually disappears. At the rim of the disc on its lower surface the lamina of each bract projects

abruptly, extending down as much as 3 mm., where it practically touches the disc below nearly enclosing the sporangia (fig. 23). Any cross-section cuts the free bract tips at several levels since the tips overlap four nodes above before terminating (fig. 24). Innermost is the disc cut on the bias; next the upturned disc is still fused but with the lamina of each bract added; the next outer whorl shows free bracts without disc tissue; and the outermost whorl shows a small, nondescript bract tip. There is some sort of imbricate pattern of the bracts, but since they are superposed, the pattern must be due to local displacement of free tips.

Sporangiophores arise in bract axils, traverse an oblique course upwards (fig. 26), flatten out and bear 4 sporangia (fig. 27). Figure 24 is a cross-section of the cone on a 30-degree slope, which shows sporangia from a somewhat tangential view. The number of radial rows of sporangia approximately equals the number of bracts, and there is one sporangiophore for every two radial rows of sporangia. Thus it is inferred that the number of sporangiophores is one-half that of the number of bracts. At this level the axis has 30 fascicular segments, each of which presumably gives off one sporangiophore as in other *Palaeostachya* species described by Renault (1882) and Hickling (1907). Hence, there must be about 60 bracts per whorl at this level, which cuts through this cone at its full width. Whether sporangiophores alternate or are superposed on bracts cannot be determined. Sporangia fill most of the space between whorls of bracts and must have been $5 \times 2 \times 2$ mm. in size. The wall is made of a single layer of cells which are somewhat elongated in surface view.

This species is heterosporous. Microspores and megaspores have spherical shape; their walls are thin, psilate and tend to fold; and the triradiate mark is small—all of these characters placing them in the genus *Calamospora* Schopf, Wilson & Bentall (1944). In coal ball no. 839 only microspores are found, which measure from 60 to 80 μ in diameter. The type cone in coal ball no. 860 has microspores of the same size (fig. 28), and in one spot near the tip are some scattered megaspores 180 μ in diameter (fig. 29). In the cones from coal balls nos. 882 and 858 only megaspores are present (fig. 30), and they are badly shattered so that isolation is impossible. These megaspores vary from 250 to 280 μ in diameter. In no. 882 are associated structures that may be microspores, but owing to poor preservation it is not possible to observe definite spore characters.

As Hartung (1933) has pointed out, heterospory in the calamites is rather frequent. Indeed, this family shows more incipient heterospory than any other in the plant kingdom in terms of relative frequency and the fact that microspores and megaspores never differ as much in size as do those in other heterosporous groups. Considering such observed frequency, it is puzzling that the calamites did not reach the "seed" habit as did the lepidodendroids. Apparently *Palaeostachya multifolia* was a species in a transition to heterospory, for the only specimen giving positive evidence of heterospory in the same cone has megaspores considerably smaller than those in cones containing megaspores only, assuming that the latter are true megasporangiate cones having reached the limit of heterospory observed in the calamites.

Coal ball no. 961 contains a cone that is notable because its developing apex is preserved. The length of the whole shoot is about 10 cm. Organization of the axis and bracts places it clearly within this species even though there is no trace of any sporangia. There are some associated structures that might be spores, but they do not possess definite spore characters. This specimen checks point for point with *Calamites multifolia* Reed, and since it is a developing shoot, as is Reed's, its identity is evident. Total size, presence of forty leaves per whorl fused basally into a disc, bract size, shape, and organization are features in common. There is also grouping of fascicular segments into pairs, which Reed noted as a feature of *Palaeostachya vera* Seward. Therefore, it seems apparent that Reed's twig is a developing cone in which sporangia were not yet developed or destroyed in fossilization.

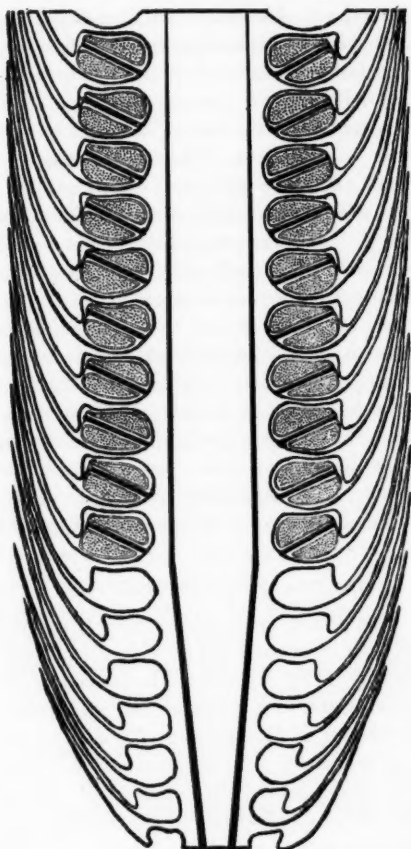
The meristem itself is worthy of note since so few are known in paleobotany. The first peel to show the shoot apex reveals no less than 11 surrounding whorls of leaves in various developmental stages (fig. 31). Cells of the apex are isometric, about 30 μ in diameter, and show a tendency to periclinal division toward the shoot margin. Immediately below this region the tissue appears to be crushed from one side; but 1 mm. below the apex this distortion disappears, the shoot has nearly reached full width, a hollow pith cavity has formed, and even vascular tissue has begun to differentiate. Such a blunt apex is very similar to that of *Equisetum*. Further development shows that once primary xylem is formed, its position or distance from the shoot center does not change with the addition of secondary wood. A problem arises in accounting for the difference between the number of fascicular segments and the number of bracts at a given node. In this species there are about 30 segments and 40 bracts per whorl. In calamites there is usually one leaf trace given off per segment, but favorable sections of this cone show three traces developing from some pairs of fascicular segments. In this way an appropriate increase in leaf trace and bract number occurs.

Since all the specimens are shattered or fragmentary, a drawing is appended to give a better visual impression of the morphology and proportions of this cone (text-fig. 1).

Diagnosis.—Cone 8 cm. long and 3 cm. wide, tapering to 1.5 cm. near the base; axis 1 cm. wide with hollow pith cavity, 30 fascicular segments grouped in pairs, each with protoxylem canal and secondary wood; bracts 40–60, whorled at nodes and fused into a lateral disc around the axis, and with tips upturned, free and 1.5 cm. long; sporangiophores 30 at node, inserted at level of upper bract surface, and bearing 4 pendant sporangia; heterosporous with microspores 60–80 μ and megaspores 190 to 280 μ in diameter; spores of genus *Calamospora*.

Type specimen: Coal ball no. 860, Henry Shaw School of Botany, Washington University, St. Louis, Missouri.

Locality, horizon and age: Berryville, Illinois; Calhoun coal, upper McLeansboro group; Upper Pennsylvanian.



Text-fig. 1. Longitudinal reconstruction of *Palaeostachya multifolia* based upon specimen in coal ball no. 860, $\times 2$.

Other specimens and localities:

1. Coal ball nos. 834, 843, 858, 961; Berryville, Illinois.
2. Coal ball no. 839; Booneville, Indiana.

PALAEOSTACHYA SP.

The following description is based upon a single specimen in a coal ball from What Cheer, Iowa. Its structures are obscured considerably by pyrite, and most tissue appears partly decomposed. Strangely, cortical tissues are present while most of the tracheids have disappeared. The cone is 5 cm. long and 2 cm. wide. Its axis is 5 mm. in diameter, rather slender for a cone as large as this, and is set with

whorls of 24 bracts spaced 4.5 mm. apart. In three nodes studied, 14 sporangiophores arise somewhat above and between the bracts. One sporangiophore presumably develops from one fascicular segment of the main axis and terminates in a fleshy, cruciate structure bearing 4 sporangia. Sporangia contain microspores 75–100 μ in diameter belonging to the genus *Calamospora*.

A point of interest is the relationship between number of bracts and of sporangiophores at a node. In this specimen 24 bracts and 14 sporangiophores are counted at each node. Also sporangiophores seem to come off the axis in pairs, probably a consequence of their parent segments in the main axis being grouped in pairs. In several observed instances each sporangiophore of a "pair" is placed on each side of a given bract. This further complicates the picture so that no possible symmetrical arrangement of 24 bracts and 14 sporangiophores at a node can be devised. It follows that no exact relationship exists between bract and sporangiophore number; thus tending to support Hickling's (1907) theory that sporangiophores belong to a separate node that moved downward phyletically to coincide with the bracteate node. It was also observed that sporangiophore number is controlled by fascicular segment number (one segment gives off one sporangiophore) while bract number is not rigidly controlled by segment number, as demonstrated in *P. multifolia*, thus accounting for the independence of bract and sporangiophore number.

STRATIGRAPHIC CORRELATIONS

While there have been stratigraphic correlations of plant impression fossils, made chiefly in Europe, very little work has been done with petrified plant remains found in coal balls. Schopf (1941) compared horizons of various American coal ball localities with each other and with European coal ball horizons as a background for his stratigraphic discussion of *Mazocarpon*. To date no general stratigraphic correlation of megafossil species has been prepared which would supplement spore studies in solving stratigraphic and floristic problems of past ages. If the paleobotanists studying coal balls could cooperate in a publication giving the results of their researches, a general picture of vertical and horizontal distribution of megafossil species might be obtained. The following is a very meagre contribution toward this end, involving only petrified calamitean species described in this investigation and those reported by Andrews (1952).

Calamitean remains were recovered from the following coal ball localities, all of which occur in Middle or Upper Pennsylvanian deposits.

1. What Cheer, Iowa; Des Moines series.
2. Atlas Mine, near Oskaloosa, Iowa; Des Moines series.
3. Argus Mine, near Oskaloosa, Iowa; Des Moines series.
4. West Mineral, Kansas; Fleming coal, Cherokee shale, Des Moines series.
5. Red Ray Mine, Freeburg, Illinois; No. 6 coal, Carbondale group.
6. Pyramid Mine, Pinckneyville, Illinois; No. 6 coal, Carbondale group.
7. New Delta, Illinois; No. 6 coal, Carbondale group.

8. Nashville, Illinois; No. 6 coal, Carbondale group.
9. Dix, Illinois; Calhoun coal, McLeansboro group.
10. Berryville, Illinois; Calhoun coal, McLeansboro group.
11. Booneville, Indiana; Petersburg coal No. 5, Petersburg series.
12. St. Wendells, Indiana; near Parker coal, Conemaugh series.

Species and their localities are listed below:

Arthropityx communis: West Mineral, Berryville and Atlas Mine. This species has a considerable vertical distribution comparable to that in Europe.

Arthropityx communis var. *septata*: Berryville.

Arthropityx gigas: Booneville. This horizon is considerably below that of European horizons, uppermost Carboniferous and lowermost Permian, from which this species has been reported.

Arthropityx bistriata: Booneville. Conditions here as with *A. gigas*.

Arthropityx Hirmeri: Pinckneyville. This horizon is somewhat above the Katharina deposits of the Ruhr from which this species was first reported.

Artbroxylon Williamsonii: What Cheer, Argus Mine, and West Mineral. These localities are probably near the same level and above the Lower Coal Measures of England from which this species was reported earlier.

Astromyelon Williamsonii: Berryville and St. Wendells. These localities are near the same level and much higher than the Lower Coal Measures of England from which this species was first reported.

Astromyelon cauloides: Berryville and St. Wendells.

Astromyelon pluriradiatum: Berryville.

Arthropityx illinoensis: Berryville, Red Ray, Dix and Nashville. This species appears to have a reasonably wide vertical distribution but so far is confined to central Illinois.

Arthropityx versifoveata: West Mineral.

Arthropityx kansana: West Mineral and Booneville. Booneville is somewhat above West Mineral stratigraphically and several hundred miles away, giving this species a wide distribution.

Calamites rectangularis: Berryville.

Palaeostachya multifolia: Berryville, Booneville and Harrisburg, Indiana (Reed). This cone species has some vertical distribution, and the Booneville locality is at the same level as Harrisburg, from which Reed recovered a vegetative base of this cone.

ACKNOWLEDGMENTS

The writer is very grateful to Dr. Henry N. Andrews for his guidance and assistance during this investigation. Grateful acknowledgment is also made to Dr. Wilson N. Stewart, Department of Botany, University of Illinois; Dr. Robert M. Kosanke, Illinois Geological Survey; and Dr. Robert W. Baxter, Department of Botany, University of Kansas, for their generous donations of calamitean specimens used in this study.

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EXPLANATION OF PLATE 20

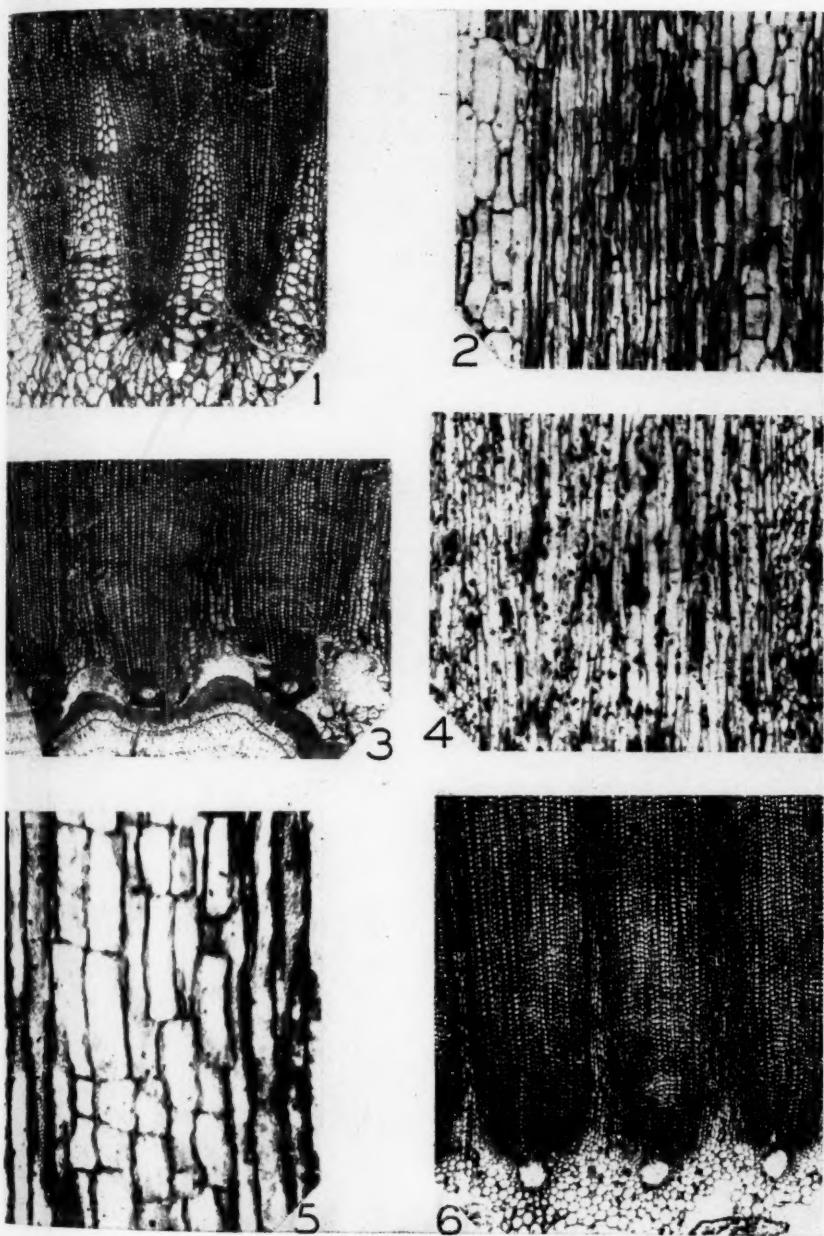
Figs. 1 and 2. *Astromylon cauloides* Anderson: Fig. 1. Cross-section of portion of large root. Coal ball no. 853. Peel 853. $\times 14$; fig. 2. Tangential section of wood near pith showing wood sector and primary rays. Coal ball no. 853. Slide 2360. $\times 28$.

Fig. 3. *Arthropityx illinoensis* Anderson. Cross-section of inner wood portion. Coal ball no. 947. Peel 947. $\times 12$.

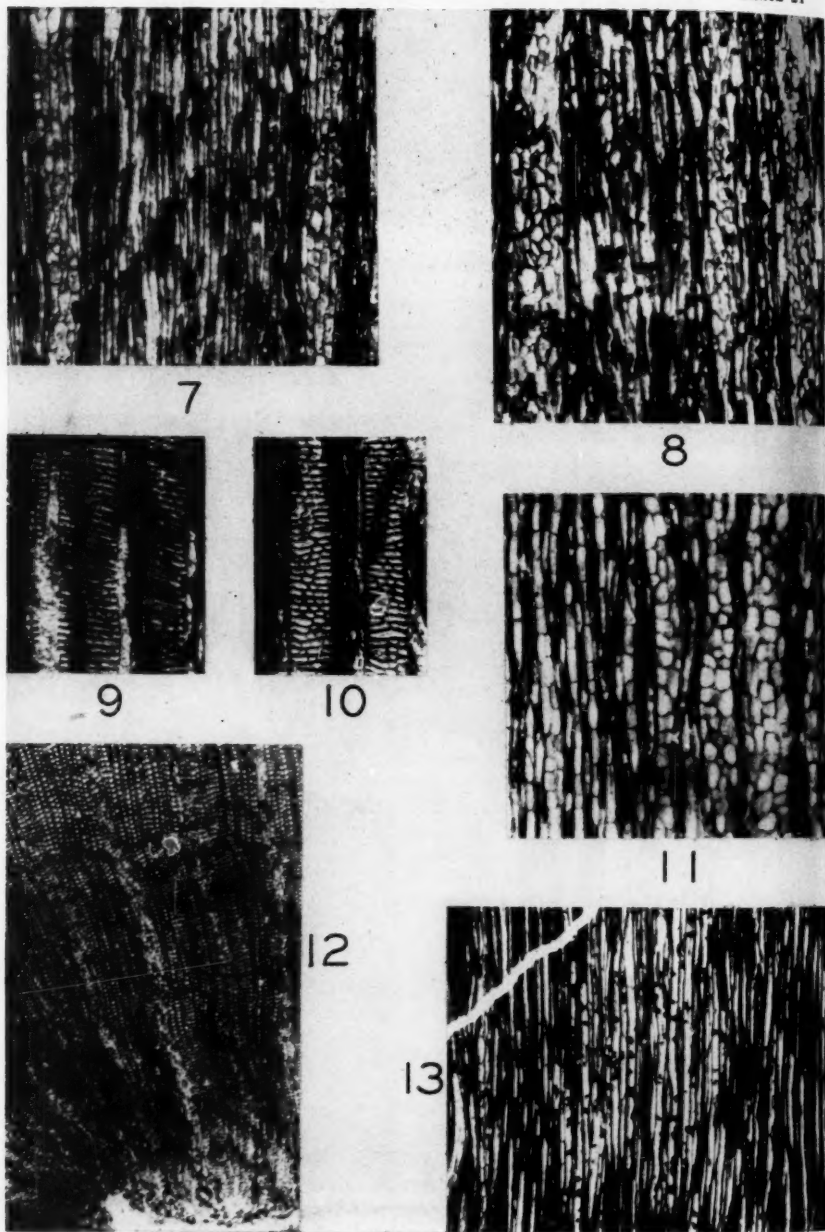
Fig. 4. *Arthropityx versifoveata* Anderson. Tangential section of wood showing wood sector and primary rays. Coal ball no. 829. Slide 2356. $\times 31$.

Fig. 5. *Arthropityx illinoensis*. Radial section of wood showing secondary ray cells and tracheids. Coal ball no. 947. Slide 2358. $\times 75$.

Fig. 6. *Arthropityx versifoveata*. Cross-section of inner wood portion. Coal ball no. 829. Peel 829. $\times 14$.



ANDERSON—AMERICAN PETRIFIED CALAMITES



ANDERSON—AMERICAN PETRIFIED CALAMITES

EXPLANATION OF PLATE 21

Fig. 7. *Arthropityx illinoensis* Anderson. Tangential section of wood near the pith showing wood sector and primary rays. Coal ball no. 947. Slide 2357. $\times 28$.

Fig. 8. *Arthropityx* sp. Tangential section of outer wood showing tracheids, primary rays and a large secondary ray. Coal ball no. 957. Slide 2359. $\times 33$.

Figs. 9 and 10. *Arthropityx versifoveata* Anderson. Pitting in radial walls of tracheids. Coal ball no. 753. Slide 1924. $\times 133$.

Fig. 11. *Astromylon pluriradiatum* Anderson. Tangential section of wood. Coal ball no. 959. Slide 2363. $\times 28$.

Fig. 12. *Arthropityx* sp. Cross-section of wood portion showing sectors and undiminishing primary rays. Coal ball no. 957. Peel 957. $\times 11$.

Fig. 13. *Artroxylon Williamsonii* Reed. Tangential section of wood showing short-celled secondary rays in woody and fibrous zones. Coal ball no. 946. Slide 2354. $\times 16$.

EXPLANATION OF PLATE 22

Calamites rectangularis Anderson (except fig. 17)

Fig. 14. Nodal cross-section near apex of shoot showing departure of whorled leaves. Coal ball no. 834. Slide 2366. $\times 42$.

Fig. 15. Cross-sections of leaves. Coal ball no. 860. Slide 2368. $\times 39$.

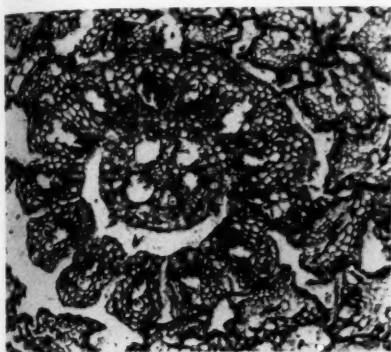
Fig. 16. Longisection of shoot. Coal ball no. 879. Peel 879A-tan 11. $\times 6$.

Fig. 17. *Astromylon cauloides* Anderson. Cross-section of small root. Coal ball no. 882. Peel 882A. $\times 7$.

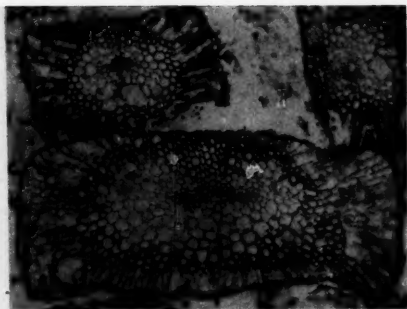
Fig. 18. Cross-section of small stem. Coal ball no. 860. Peel 860J-t1. $\times 11$.

Fig. 19. Cross-section of large twig. Coal ball no. 860. Slide 2367. $\times 21$.

Fig. 20. Cross-section of small twig. Coal ball no. 960. Slide 2364. $\times 44$.



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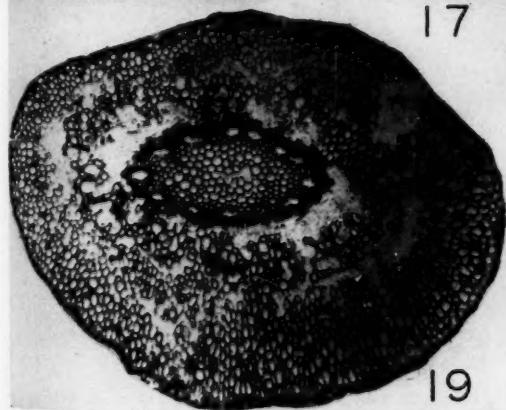
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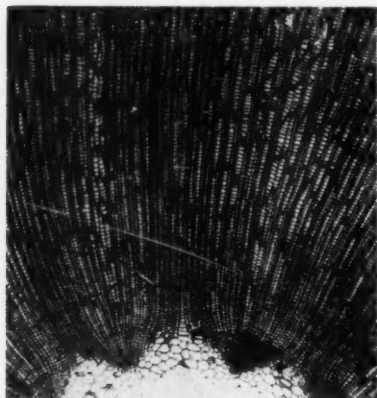


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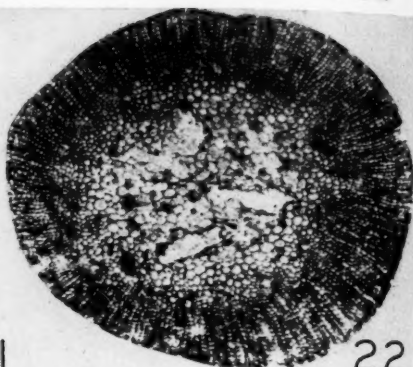


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EXPLANATION OF PLATE 23

Fig. 21. *Astromylon pluriradiatum* Anderson. Cross-section of root. Coal ball no. 959. Peel 959. $\times 7$.

Figs. 22-24. *Palaeostachya multifolia* (Reed) Anderson.

Fig. 22. Cross-section of axis at lowermost level. Coal ball no. 860. Slide 2370. $\times 19$.

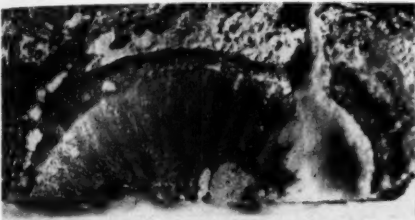
Fig. 23. Longisection of cone. Coal ball no. 860. Peel 860D-tan 20. $\times 4$.

Fig. 24. Cross-section of cone. Coal ball no. 860. Peel 860C-b10. $\times 6$.

EXPLANATION OF PLATE 24

Palaeostachya multifolia (Reed) Anderson

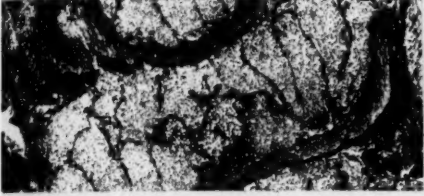
- Fig. 25. External view of upper surface of bract whorl. Coal ball no. 858. $\times 3$.
- Fig. 26. Tangential section of cone showing fused bracts, sporangia, and sporangio-phores. Coal ball no. 860. Peel 860C-tan 17. $\times 6$.
- Fig. 27. Radial section of sporangia attached to upper tip of sporangiophore. Coal ball no. 839. Peel 839A2b-tan 1. $\times 12$.
- Fig. 28. Spore isolated from coal ball no. 860. Slide 2372. $\times 530$.
- Fig. 29. Scattered microspores and megaspores in sporogenous region. Coal ball no. 860. Slide 2369. $\times 29$.
- Fig. 30. Tangential section of sporangia with megaspores. Coal ball no. 858. Peel 858C1-tan 6. $\times 10$.
- Fig. 31. Cross-section of cone through developing apex. Coal ball no. 961. Peel 961A-X11. $\times 6$.



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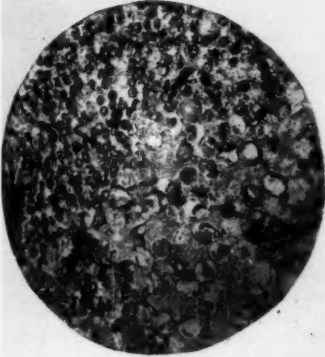
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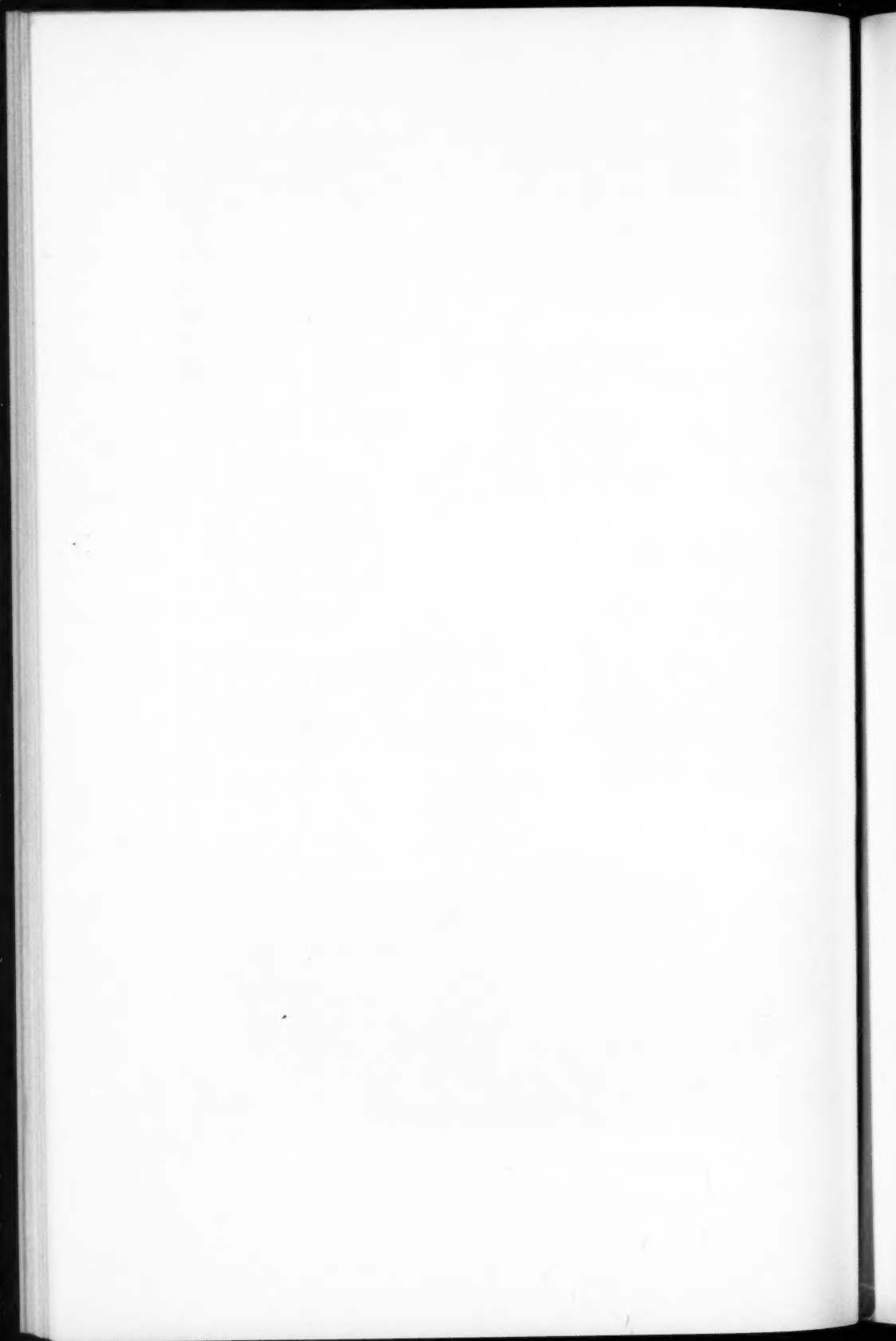


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